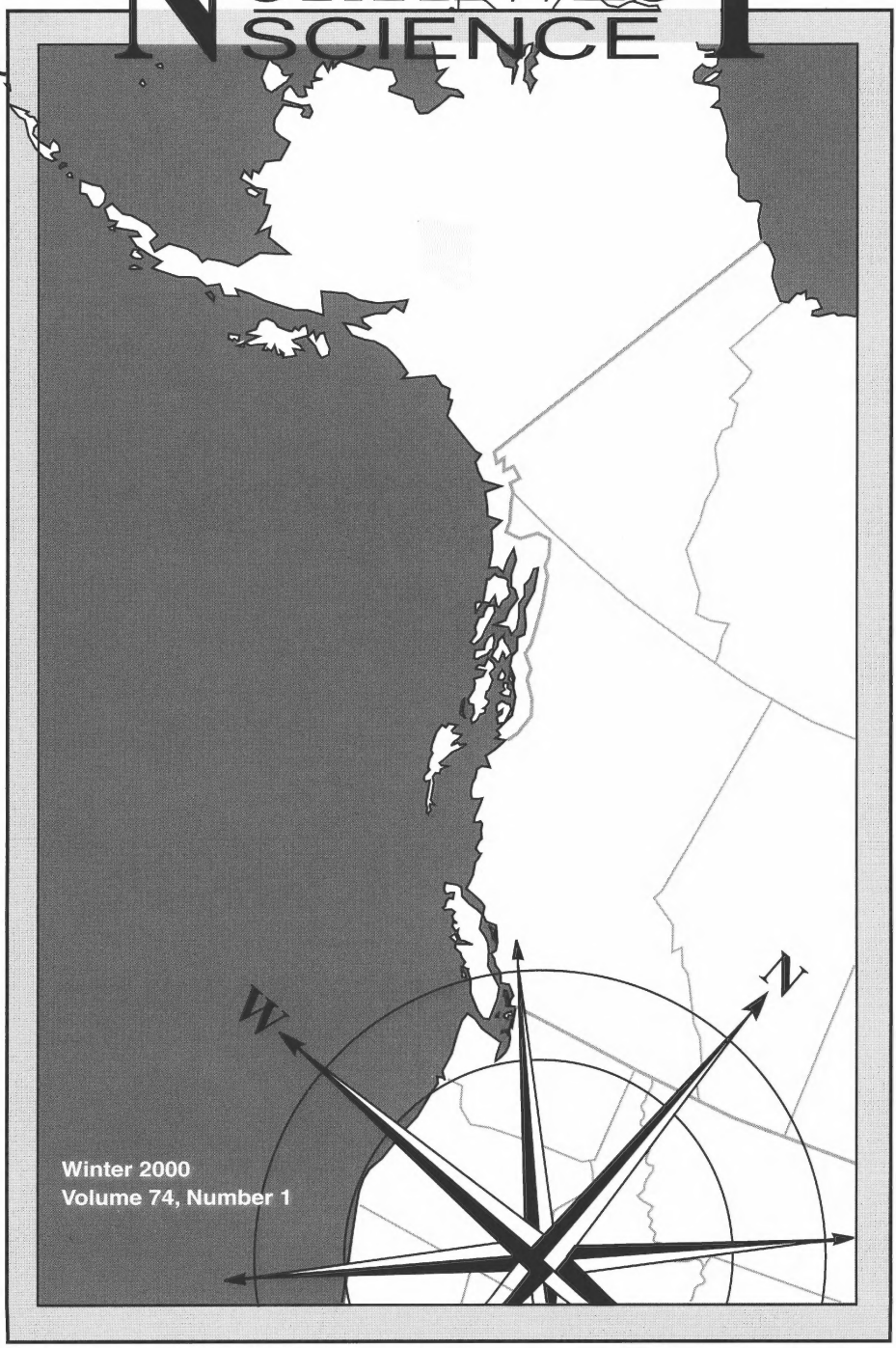
NORTHWEST SCIENCE



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A Note from the Editor

Welcome to the Y2K. It seems we have all survived unscathed. This is the 74th volume of *Northwest Science*—truly an amazing accomplishment for a small society dedicated to the advancement of science in the Pacific Northwest. Readers and authors should note that I have made several modifications to the "Information for Authors." The main differences are in the Literature Cited section where there are a few changes in the format. Please look these over before submitting manuscripts. In addition, we have changed to a Winter, Spring, Summer, and Fall format rather than February, May, August, and November. This gives us a little more flexibility in getting our issues out in a timely fashion.

I am pleased to report that the number of manuscripts submitted to *Northwest Science* increased substantially in 1999. The number of manuscripts received by the Editor averaged 44.5 from 1993 to 1998 (range 37–49) and increased to 65 in 1999 (Figure 1). I have already received 15 manuscripts as of mid-February this year. My guess is that we will maintain the increased rate of submissions this year as well. The manuscript rejection from 1997 to 1998 has been about 34 percent.

As we enter a new millennium, I think it is appropriate to acknowledge the people who have made a genuine difference in making *Northwest Science* what it is today. First of all, thank you to the members of the Northwest Scientific Association—you are ultimately responsible for the continuation of the society and our fine journal—keep the faith. Heartfelt thanks go to our Associate Editors. Your dedication to maintaining and improving the high quality of our published papers is sincerely appreciated. I know it is a lot of hard work finding reviewers, editing papers, and keeping up with the Editor's demand for a short turnaround time. Thank you also to our reviewers of manuscripts—you are the unsung heroes. Special thanks are due to our Managing Editor, Nancy Grunewald. The exceptionally high quality of the layout of articles is very much appreciated (and noticed) by our authors and by me. I also want to acknowledge my secretary, Janice Cimmer; she is of immense help in keeping the manuscripts and galley proofs moving along. Others who contribute substantially to *Northwest Science* include David L. Peterson for his help in soliciting articles for the Forum and Randall C.

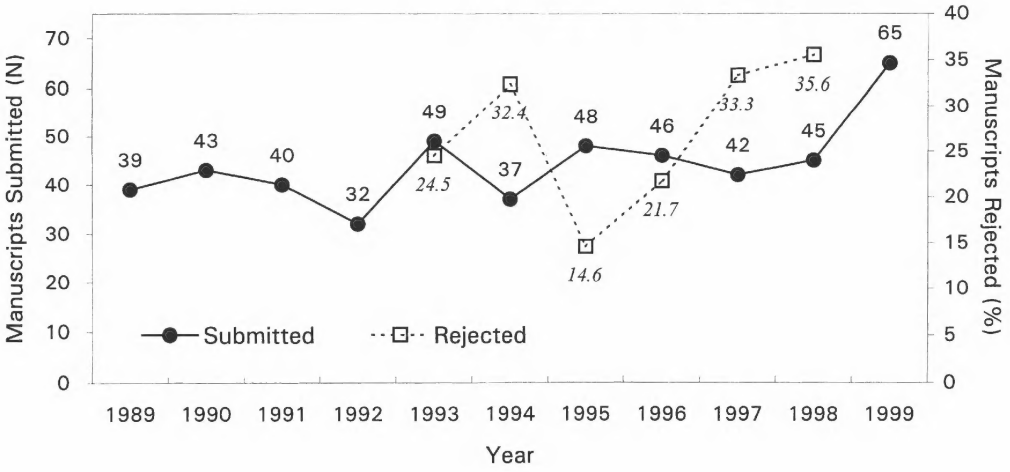

Figure 1. *Northwest Science* manuscript submissions and rejections, 1989–1999.

Morris for book reviews. I would also like to thank members of the Board of Trustees and officers of the Association—your hard work on behalf of the Association is valued. Lastly, and certainly not least, thanks are due to our authors for continuing to submit high quality manuscripts—keep up the good work; it really is a pleasure to work with you.

There are a number of topics I think will be particularly significant in the Pacific Northwest during the next few years if not decades. These include but certainly are not limited to:

- The role of marine-derived nutrients in terrestrial and freshwater aquatic ecosystems and how these nutrients "feed back" to marine systems.
- Determining how to manage ecosystems in a manner that both maintains system integrity and simultaneously provides needed commodities such as timber, fish, and water.
- Understanding how global climate change affects the functioning of Pacific Northwest ecosystems and how they are managed.
- Gaining a far better understanding of the importance and role of mycorrhizal fungi in forested and non-forested ecosystems.
- Figuring out how to conduct long-term ecological monitoring at different spatial and temporal scales.
- The role of bryophytes, lichens and liverworts in Pacific Northwest ecosystems—both as indicators of change and as vital system components.
- The long-term viability of wildlife populations as habitats become increasingly fragmented.

I certainly hope to see manuscripts submitted on these topics (and others) in the near future.

Finally, I strongly encourage members of the Northwest Scientific Association to solicit new members and to submit more manuscripts—spread the word. Equally, I urge our non-member readers to join the Association and support science in the Pacific Northwest.

With Best Regards,
Edward G. Schreiner
Editor

Erratum

Please note that requests for reprints of the paper "The encroachment of exotic herbaceous plants into the Olympic National Forest" by Charles W. Heckman (*Northwest Science* November 1999, 73(4):264-276) should be made to: PHC, Inc. Attn: Linda/PNW, 5312 NE 148th Street, Portland, OR 97230. Please refer to Distribution Number 98-187BE. Charles W. Heckman's current address is 315 – 93rd Ave SW, Olympia, WA 98512-9101.

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Influence of Western Juniper Development on Distribution of Soil and Organic Layer Nutrients

Abstract

The purpose of this study was to determine effects of invading western juniper (*Juniperus occidentalis* Hook.) into big sagebrush (*Artemisia tridentata* Nutt.)/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith [now *Pseudoroegneria spicata*]) ecosystems of central Oregon on spatial distribution of nutrients in organic and mineral soil layers. The organic layer and mineral soil from four layers (0-5, 5-15, 15-30, and 30+ cm), were collected beneath juniper trees of five size classes, and one area devoid of juniper on five replicated sites. Samples were taken at five distances (0 to 4 canopy radii) from tree boles into intercanopy areas. The organic layer and mineral soil were analyzed for organic carbon (C_{org}), total nitrogen (N), total phosphorus (P) and total sulfur (S); mineral soil was analyzed for exchangeable calcium (Ca_{ex}), magnesium (Mg_{ex}) and potassium (K_{ex}). Mass of the organic layer and amounts of organic layer nutrients increased with juniper size, and were higher under canopies than in intercanopy and no juniper areas. Concentrations of organic layer N, P, and S declined with distance from tree boles. Tree size, distance and soil layer interacted to affect concentrations of soil C_{org}, K_{ex}, Ca_{ex} and Mg_{ex}. Concentrations of soil N and S increased with tree size. Amounts of soil nutrients, except C_{org}, were not significantly influenced by tree size, but amounts of all soil nutrients, except S and Ca_{ex}, were greater under juniper trees than intercanopy areas. Only Ca_{ex} and Mg_{ex} appeared to have been lost from intercanopy soils compared to no juniper soils.

Introduction

In eastern Oregon and over much of its range, western juniper (*Juniperus occidentalis* Hook.) has encroached into big sagebrush (*Artemisia tridentata* Nutt.)/bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith [now *Pseudoroegneria spicata*]) communities (Caraher 1978, Eddleman 1987). Recently juniper and pinyon species have increased throughout pinyon-juniper woodlands of the western United States (Miller and Wigand 1994). Tree and shrub invasion in arid and semiarid regions results in formation of "fertile islands" where soil and organic layer properties vary spatially away from plant centers to adjacent interspaces. Development of spatial patterns has been largely attributed to rooting and litterfall patterns of trees or shrubs (Fireman and Hayward 1952, Charley and Cowling 1968, Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Charley and West 1975, Barth 1980). However, the enriched island effect is complex, and owes its occurrence to many biotic and abiotic factors and their interactions, induced by presence of trees or shrubs (Leopold 1933, Garcia-Moya and McKell 1970, Tiedemann et al. 1971, Tiedemann and Klemmedson 1973, Balandreau et al. 1976, Tiedemann and Klemmedson 1977, Barth 1980, Tiedemann and Furniss 1985, Belksy et al. 1989, Belsky 1994).

Where roots extend beyond the canopy edge, as in the case of western juniper (Young et al. 1984, Everett et al. 1986), trees or shrubs may exploit moisture and nutrients from interspaces (Klopatek 1987, Bernhard-Reversat 1982). Nonetheless, trees in semi-arid (Bernhard-Reversat 1982), tropical, and subtropical (Belsky 1994) savannas of Africa, and shrubs in the American deserts (Garcia-Moya and McKell 1970, Romney et al. 1978) are thought to be major factors in maintaining soil fertility and productivity of the systems they inhabit.

The rationale for this study was to understand the role of western juniper in nutrient-productivity relations of the ecosystem it dominates just east of the Cascade Range. We examined the influence of invasion of western juniper into the sagebrush/grass system on nutrient status of soil and organic layers of the larger system, i.e. the

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complex of juniper trees and intercanopy areas occupied by sagebrush/grass. In particular, we sought to determine (1) if juniper encroachment changes the spatial distribution of nutrients in juniper and intercanopy areas relative to areas without juniper, and (2) the extent of changes with size (age) of individual juniper trees.

Study Area

The study area was the Three Springs Ranch located about 11 km southwest of Prineville (1110 m elevation) in central Oregon. This area is typical of the community dominated by western juniper on the western edge of the Central Oregon Plateau at the lower boundary of the ponderosa pine zone (Driscoll 1964). Climate is continental with maritime influence from storms originating off the Pacific coast. The region is semiarid with dry, hot summers and cold winters. Precipitation, averaging 26.6 cm annually, occurs as snow during winter and rain during spring and fall. Mean annual temperature at Prineville is 8.5°C; mean January and July temperatures are 0°C and 18.2°C, respectively (National Oceanic and Atmospheric Administration 1995).

Soils are young and derived from volcanic ash from the eruption of Mt. Mazama 6845 ± 45 years ago (Bacon 1983). Basalt of local origin underlies the ash (United States Department of Agriculture, Soil Conservation Service 1986). Five soils series occur in the study area: Deschutes, Stukel, Stukmond, Redmond, and Lickskillet (Personal communication, Amanda Moore, Soil Scientist, United States Department of Agriculture, Natural Resources Conservation Service, Redmond, Oregon). Observations of depth, texture, and horizon development during sampling indicated that our sites were primarily in the Stukel series. These soils are well-drained, shallow (25 to 50 cm) loamy, mixed, superactive, mesic Lithic Haploxerolls (United States Department of Agriculture, Natural Resources Conservation Service 1999). No apparent buried soil exists over the basalt bedrock. Outcrops of basalt occur as blisters scattered throughout the gently undulating terrain.

Vegetation of the juniper understory, intercanopy, and areas without juniper is dominated by big sagebrush, rabbitbrush (*Chrysothamnus spp.*), bluebunch wheatgrass, and Idaho fescue (*Festuca idahoensis* Elmer). Cover of juniper understory, intercanopy, and areas without juniper averages about 25% but is highly variable.

Methods

Conceptual Approach and Site Selection

The general equation of state factors (Jenny 1961):

$$s = f(cl, o, r, p, t) \quad (1)$$

provided a formalistic approach for the field study. The equation states that magnitude of any soil property (s) is a function of climate (cl), the biotic factor (o), relief (r), parent material (p), and time (t). Revision of the equation as follows:

$$s_n = f(\mathbf{o}_j, cl, o, r, p, t,...) \quad (2)$$

$$s_n = f(\mathbf{t}_j, cl, o, r, p, t ...) \quad (3)$$

provides a conceptual model for site selection and field sampling to determine the influence of western juniper trees ($\mathbf{o}_j$) and their relative size (age) or time of occupancy of a specific site($\mathbf{t}_j$) on any nutrient property (s_n) of the soil or organic layer.

The remaining state factors in the equations were controlled by selecting study sites so that variation in these factors would have little influence on the dependent variable s_n, compared to that of the variable state factors, $\mathbf{o}_j$ and $\mathbf{t}_j$. Climate, topography (2-5% uniform eastward slope), parent material and age of developed soils were uniform among and within sites. Impact of the biotic factor (o), other than juniper trees (i.e., understory vegetation, herbivores, human activity, including fire) appeared to be slight; in no case was distribution of these biotic subfactors related to juniper presence or size. Vegetative cover of shrubs and herbs was sparse, but variable, moreso in intercanopy areas and areas without juniper. Although shrubs and herbs may influence distribution of soil and organic layer nutrients (Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Klemmedson 1983), the scale of this influence is small compared to that of western juniper and was minimized by increasing plot size in the intercanopy area. This portion of Three Springs Ranch showed no evidence of livestock grazing. Length of time the area had been excluded from grazing was not possible to determine. However, there was a well- developed organic layer beneath mature trees and no evidence of livestock trampling or feces. This suggested that grazing had been excluded for a long period of time. Signs of human activity were sparse.

TABLE 1. Ages and physical characteristics of five size classes of western juniper trees sampled in this study.

Size Class	Age (yr)		Height (m)		Basal Diameter (cm)		Canopy Diameter (m)	
	Ave.	Range	Ave.	Range	Ave.	Range	Ave.	Range
1	36	21-58	3.3	2.9-3.8	13	11-17	1.7	1.6-2.2
2	55	37-68	4.8	4.1-6.0	22	17-26	2.5	2.1-3.3
3	62	41-85	7.0	5.7-8.2	37	29-43	4.5	3.2-5.6
4	101	44-154	9.5	8.5-11.7	49	44-53	6.3	5.3-8.7
5	161	108-231	9.9	9.2-10.4	63	58-68	6.7	5.6-7.8

From each of five noncontiguous sites, we located a pool of trees for each of five size classes (Table 1; see Figure 1 in Tiedemann and Klemmedson, 2000), then randomly selected one tree from each class for a total of 25 sample trees. In addition, we randomly selected "no juniper" sampling plots from 5 to 10 ha areas without juniper. Average age for classes 1 through 5 were 36, 55, 62, 101 and 161 years. Average height ranged from 3.3 to 9.9 m and canopy diameters from 1.7 to 6.7 m. Cross-sections from the base of trees were aged by Franco Biondi, Laboratory of Tree Ring Research, University of Arizona.

Sampling

At each sample tree, soil and the organic layer were collected at distances equal to 0, 0.5, 1, 2 and 4 radii of the tree canopy along a transect extending due north of the tree bole. At 0, 0.5, and 1 canopy radii positions the entire organic layer was collected within a 0.093 m^2 metal frame. At 2 and 4 canopy radii, a 0.5 m^2 frame was used. Below these, 5 cm diameter soil cores were collected from the 0-5, 5-15, and 15-30 cm soil layers. Two adjacent cores also were taken from the 0 to 5 cm layer for an adequate sample. Because of shallowness and variability in soil depth to the basalt (35 to 65 cm depth), grab samples were taken below 30 cm.

Laboratory and Statistical Analyses

Soil and organic layer samples were air-dried. Soil was sieved to remove coarse fragments >2-mm diameter and ground to pass a 0.15-mm sieve. Organic layer samples were ground to pass a 0.425-mm sieve. Samples were analyzed for organic carbon (C_{org}) by dry combustion (Nelson and Sommers, 1982) in a Leco high-frequency induction furnace (Leco Corp., St. Joseph, MI). Total nitrogen (N) was determined by semi-micro-Kjeldahl (Bremner and Mulvaney, 1982) and total sulfur (S) by dry combustion in the Leco high-frequency induction furnace (Tiedemann and Anderson, 1971). Total phosphorus (P) was determined with ascorbic acid color development (Olsen and Sommers, 1982) following hydrofluoric acid digestion (Bowman, 1988). Exchangeable calcium (Ca_{ex}), magnesium (Mg_{ex}), and potassium (K_{ex}) of soils were determined by inductively coupled plasma emission spectroscopy (Barnes, 1977) following extraction with ammonium acetate (Thomas, 1982).

Because soil bulk density increased markedly with distance from tree boles and with soil depth (0.79 to 1.13 g/cm^3), data for both concentration and amounts of nutrients are meaningful here. Statistical analysis for soil nutrient concentration followed a split-split-plot design with size class as the main plot factor, distance from the base of the tree as the sub-plot factor, and soil layer as the sub-sub-plot factor. Amounts of soil nutrients were summed for layers of the upper 30 cm and analyzed as a split-plot with size class as the main plot factor and distance as the sub-plot factor. Analyses of mass, and concentrations and amounts of nutrients in the organic layers were similar to those for soils except there was no sub-sub-plot factor for soil layers. Two statistical analyses [SAS Institute Inc. (1987) analysis of variance] were performed for soil and organic layer nutrient concentrations and amounts for each response variable, and for mass of the organic layer. The first analysis included data for the "no juniper" sites. For this analysis, the least squares (LS) means for size and distance could not be estimated because of missing data caused by the unbalanced

design (i.e., no tree size or distance data for "no juniper" sites). Where the size X distance interaction was significant, the "no juniper" LS mean was tested along with distance means for size classes 1 through 5. The second analysis did not include the "no juniper" sites and was used where the size X distance interaction was not significant. Here the "no juniper" mean could not be compared with the distance means for classes 1 through 5. Separation of means by least significant difference (LSD)(Carmer and Swanson 1971) was performed on differences significant at $P \leq 0.05$ in the analysis of variance.

Results

Organic Layer

Size of trees and location interacted significantly ($P \leq 0.0001$) to influence mass of the organic layer. Mass of the organic layer was greatest at the base of the largest trees (class 5) and declined markedly with tree size and distance to the canopy edge. Size and distance had no effect on organic layer mass beyond tree canopies (Table 2).

The tree size X distance interaction for nutrient concentration of the organic layer was significant only for C_{org}. Wide variation in organic layer C for all tree sizes and at all distances except distance 2 explains this significant interaction. The main effect of tree size had no effect on concentrations of N, P and S in the organic layer, but the main effect of distance from tree boles significantly ($P \leq 0.0001$) influenced each of these organic layer nutrients. The effect of distance on concentrations of N and S was similar (Table 3);

TABLE 2. Mass of organic layer (kg/m^2) as a function of distance from tree boles for six tree size classes, including no juniper (0).

Tree size class	Distance from tree boles (canopy radii)				
	0	0.5	1	2	4
0	0.12^{a}[1]				
1	3.75^{cde}	1.27^{ab}	0.21^{a}	0.46^{a}	0.64^{a}
2	4.79^{defg}	2.74^{bc}	0.49^{a}	0.25^{a}	0.36^{a}
3	5.36^{efg}	3.39^{cd}	0.56^{a}	0.15^{a}	0.30^{a}
4	8.96^{h}	4.32^{cdef}	0.69^{a}	0.09^{a}	0.18^{a}
5	9.26^{h}	6.13^{fg}	0.88^{a}	0.07^{a}	0.18^{a}

[1]Values with the same letters are not significantly different at $P \leq 0.05$.

TABLE 3. Effect of distance from tree boles on concentrations (g/kg) of N, P and S in the organic layer.

Distance from tree bole (canopy radii)	N	P	S
0	11.0^{a}[1]	0.94^{a}	1.13^{a}
0.5	10.8^{a}	0.83^{b}	1.05^{a}
1	7.9^{b}	0.73^{bc}	0.83^{b}
2	7.9^{b}	0.66^{c}	0.74^{b}
4	7.8^{b}	0.64^{c}	0.82^{b}
no juniper[2]	9.0	0.74	0.89

[1] Within column values with common letters are not significantly different at $P \leq 0.05$.

[2] Because of an unbalanced design, no separation of means could be made for no juniper sites.

concentrations of these nutrients were greatest at 0 and 0.5 distances and significantly lower but similar at the canopy edge and intercanopy distances. Concentration of P in the organic layer declined more rapidly to the canopy edge, and was lower at intercanopy positions than N or S (Table 3). Concentrations of N, P, and S in the organic layer of "no juniper" areas were slightly higher than that of intercanopy areas (Table 3), but differences were not testable for significance because of the unbalanced statistical design.

Size of junipers and distance from tree boles influenced amounts of C_{org}, N, P, and S in the organic layer in similar fashion, but the size X distance interaction also was highly significant ($P \leq 0.0001$). Amounts of these nutrients beneath tree canopies increased with juniper size, especially at distance 0 (Table 4). However, at the canopy edge and beyond, size and distance had no effect on nutrient amounts. Amounts of these organic layer nutrients averaged 14 to 17 times greater near boles than at the canopy edge (Table 4).

Soil

Nutrient Concentrations

Juniper trees influenced nutrient concentration of soils more by spatial effects than by size. The three-way tree size X distance X soil layer interaction was significant ($P \leq 0.01$) for concentrations of C_{org}, Ca_{ex}, Mg_{ex} and K_{ex}. The interactions for C_{org} and Mg_{ex} are easily explained: concentration of C_{org} increased with tree size (Figure 1) beneath canopies, but decreased with soil depth and distance away from tree boles (Figures 1 and

TABLE 4. Amounts (g/m^2) of organic C, N, P, and S in the organic layer of juniper as a function of distance from tree boles for six size classes of juniper, including no juniper (0).

Size class	Distance from tree boles (canopy radii)				
	0	0.5	1	2	4
Organic carbon					
0	50^{a}[1]				
1	1032^{cd}	399^{abc}	89^{a}	106^{a}	313^{abc}
2	1712^{def}	907^{bc}	169^{a}	93^{a}	113^{a}
3	1995^{fg}	1141^{cde}	137^{a}	49^{a}	123^{a}
4	3447^{h}	1801^{ef}	191^{ab}	28^{a}	71^{a}
5	3195^{h}	2430^{g}	201^{ab}	30^{a}	43^{a}
Nitrogen					
0	1.1^{a}				
1	31.3^{bc}	10.6^{ab}	1.8^{a}	1.8^{a}	9.6^{ab}
2	56.4^{de}	30.2^{bc}	3.7^{a}	1.7^{a}	2.8^{a}
3	63.4^{ef}	36.2^{cd}	4.0^{a}	1.3^{a}	2.2^{a}
4	107.5^{g}	44.0^{cde}	5.6^{a}	0.7^{a}	1.6^{a}
5	100.7^{g}	80.8^{fg}	7.1^{a}	0.4^{a}	1.6^{a}
Phosphorus					
0	0.09^{a}				
1	2.98^{bcd}	0.15^{a}	0.26^{a}	0.90^{ab}	0.91^{ab}
2	3.60^{cd}	1.99^{abc}	0.28^{a}	0.17^{a}	0.27^{a}
3	4.76^{de}	2.71^{bcd}	0.51^{a}	0.12^{a}	0.21^{a}
4	9.73^{f}	3.03^{bcd}	0.54^{a}	0.06^{a}	0.15^{a}
5	10.59^{f}	6.36^{e}	0.72^{ab}	0.04^{a}	0.12^{a}
Sulfur					
0	0.11^{a}				
1	3.70^{cd}	1.26^{abc}	0.17^{a}	0.25^{a}	0.82^{abc}
2	5.41^{ef}	2.78^{bcd}	0.42^{ab}	0.19^{a}	0.30^{a}
3	6.60^{fg}	3.62^{cde}	0.46^{ab}	0.10^{a}	0.18^{a}
4	10.06^{hi}	3.84^{de}	0.62^{ab}	0.06^{a}	0.17^{a}
5	11.68^{i}	8.26^{gh}	0.65^{ab}	0.04^{a}	0.14^{a}

[1]Values within each nutrient group with the same letters are not significantly different from each other at $P \leq 0.05$.

TABLE 5. Concentrations (g/kg) of exchangeable Ca and Mg in the 0–30 cm soil layer as a function of distance from tree boles for six size classes of juniper, including no juniper (0).

Size class	Distance from tree boles (canopy radii)				
	0	0.5	1	2	4
Ca_{ex}					
0	1.66[1]				
1	1.50^{c-g}[2]	1.72^{h}	1.70^{h}	1.83^{h}	1.41^{bcd}
2	1.60^{d-g}	1.44^{b-e}	1.39^{bcd}	1.41^{bcd}	1.52^{fgh}
3	1.61^{efg}	1.49^{c-g}	1.45^{b-f}	1.44^{b-e}	1.33^{abc}
4	1.96^{i}	1.68^{h}	1.45^{b-f}	1.38^{bcd}	1.28^{a}
5	1.98^{i}	1.64^{g}	1.30^{ab}	1.21^{a}	1.29^{ab}
Mg_{ex}					
0	0.38				
1	0.31^{cde}	0.31^{cde}	0.29^{abc}	0.30^{bc}	0.30^{bc}
2	0.37^{gh}	0.35^{efg}	0.34^{d-g}	0.34^{d-g}	0.32^{cde}
3	0.33^{def}	0.34^{d-g}	0.35^{efg}	0.35^{efg}	0.32^{cde}
4	0.40^{h}	0.36^{fg}	0.32^{cde}	0.32^{c-f}	0.29^{abc}
5	0.34^{d-g}	0.31^{cde}	0.27^{ab}	0.26^{a}	0.26^{a}

[1] Because of an unbalanced design, no separation of means could be made for the no juniper age class (0).
[2] Values within each nutrient group with common letters are not significantly different at $P \leq 0.05$.

2). The three-way interaction for Mg_{ex} is explained by the increasing difference in Mg_{ex} concentration among size classes with soil depth (Figure 1) and the decline in Mg_{ex} concentration at intercanopy locations for older trees (Table 5). Both K_{ex} and Ca_{ex} responded similarly to depth and distance. Differences in concentrations of these nutrients in upper soil layers beneath canopies disappeared in lower soil layers at intercanopy locations (Figure 2), while responses to depth among size classes displayed an erratic pattern for both nutrients (Figure 1). Concentrations of Ca_{ex} and Mg_{ex} for most size classes in intercanopy soils (distances 1, 2 and 4) and some canopy locations, tended to be lower than that of no juniper soils (Table 5). However, this effect, which would suggest nutrient redistribution by juniper roots, could not be tested because of the unbalanced design for this part of the study.

Concentrations of N, P and S responded significantly ($P \leq 0.0001$) to the distance X soil layer interaction. In the upper soil layer, concentrations of these three nutrients declined markedly with distance from tree boles into intercanopy space (Figure 2). With depth, however, differences among locations disappeared. The tree size X soil layer interaction was significant for concentrations of N and S. Concentration of N in surface soils declined with size of junipers (Figure 1), but with increasing soil depth this difference in N concentration disappeared. The S concentration response was similar to that for N for the upper three soil layers, but unexplained differences among trees sizes occurred in the lower soil layer (Figure 1).

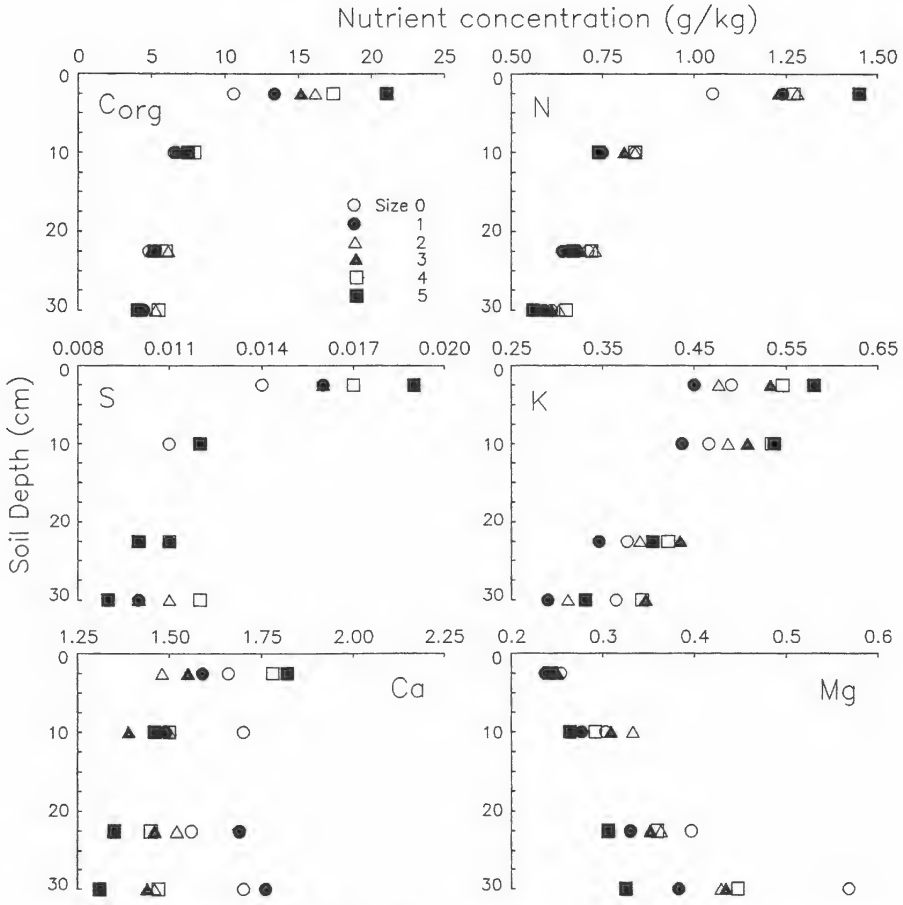

Figure 1. Concentrations of C_{org}, N, S, K_{ex}, Ca_{ex} and Mg_{ex} (averaged over distances from 0 to 4 canopy radii) as a function of soil depth for six size classes of juniper, including no juniper (0).

Interestingly, P was the only soil nutrient that did not respond to tree size, either as the main effect or as an interaction.

Nutrient Amounts

Amounts of nutrients (except S and Ca_{ex}) in the upper 30 cm of soil were significantly influenced by distance, but not by juniper size. The size X distance interaction was significant only for C_{org} ($P \leq 0.0119$). Amounts of soil C_{org} were greater for all sizes of juniper at the 0 distance and for classes 3–5 at the 0.5 distance than that for no juniper sites (Table 6), and increased with tree size. At the canopy edge and beyond, tree size had no effect on amount of soil C_{org}.

TABLE 6. Amount of organic C (kg/m^2) in the 0–30 cm soil layer as a function of distance from tree boles for six size classes of juniper, including no juniper (0).

Size class	Distance from tree boles (canopy radii)				
	0	0.5	1	2	4
0	1.88^{abc}[1]				
1	2.55^{d-h}	2.03^{a-d}	2.17^{a-e}	1.91^{abc}	1.99^{a-d}
2	3.09^{hi}	2.61^{e-h}	2.37^{b-g}	2.34^{a-f}	2.19^{a-e}
3	2.80^{fgh}	2.02^{a-d}	1.85^{ab}	2.03^{a-d}	2.02^{a-d}
4	3.59^{i}	2.91^{gh}	2.41^{c-g}	1.99^{a-d}	1.90^{abc}
5	3.62^{i}	3.08^{hi}	2.12^{a-e}	1.81^{a}	1.79^{a}

[1] Values with common letters are not significantly different at $P \leq 0.05$.

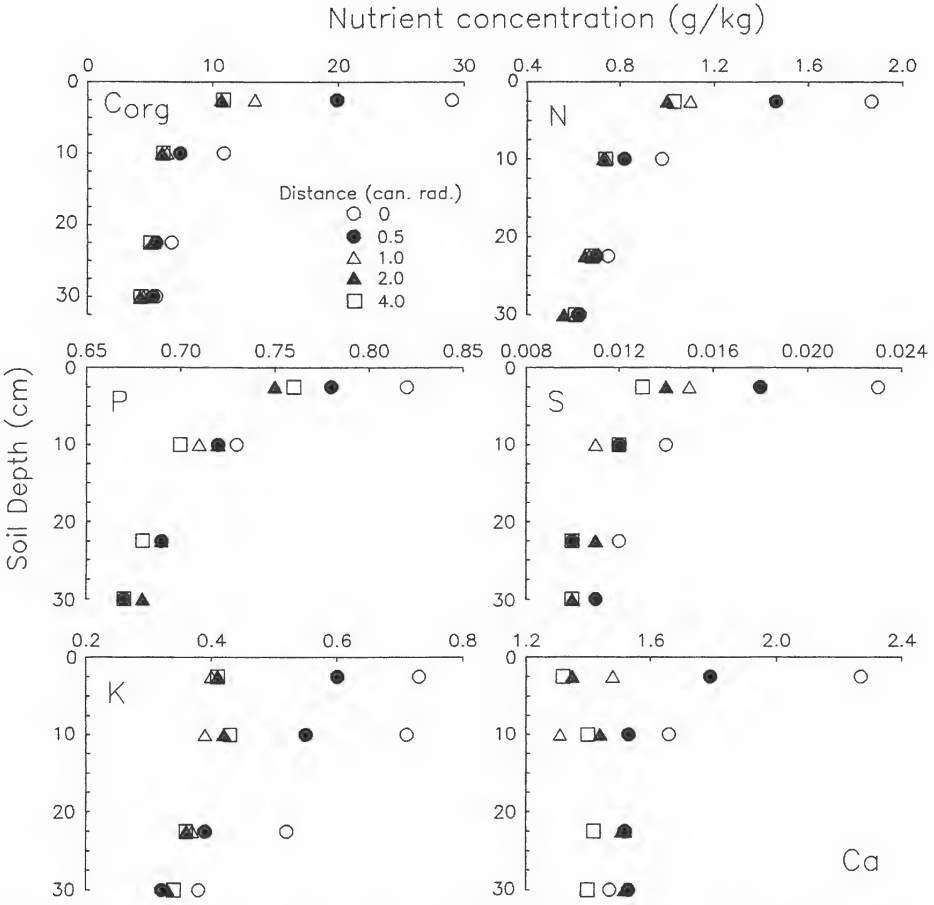

Figure 2. Concentrations of C_{org}, N, P, S, K_{ex} and Ca_{ex} (averaged over juniper size classes 1–5) as a function of soil depth for distances of 0 to 4 canopy radii from tree boles.

The distance main effect significantly influenced amounts of N, P, K_{ex} and Mg_{ex} in the 0- to 30-cm soil layer (Table 7). Amounts of N, K_{ex} and Mg_{ex} were all greater under juniper canopies, while amount of P was lower at the 0 distance than at all other distances.

Discussion and Conclusions

Juniper invasion in the sagebrush/grass ecosystem distinctly altered the spatial distribution of nutrients in the organic layer and soil. Moreover, tree size intensified this effect. Nutrient gains under juniper (exceptions noted below) were not matched with equal losses from intercanopy areas. Because

TABLE 7. Amounts (g/m^2) of total N and P, and exchangeable K and Mg in the 0–30 cm soil layer as a function of distance from tree boles.

Distance	N	P	K_{ex}	Mg_{ex}
0	277.2[b][1]	209.8[b]	174.7[b]	100.1[c]
0.5	266.2[b]	224.3[a]	148.1[a]	104.0[c]
1	243.9[a]	228.5[a]	123.2[a]	99.1[bc]
2	236.1[a]	231.2[a]	126.2[a]	97.3[ab]
4	243.0[a]	227.1[a]	127.9[a]	92.4[a]
no juniper[2]	242.4	217.6	130.7	106.9

[1] Within column values with common letters are not significantly different at $P \leq 0.05$.

[2] Because of an unbalanced design, no separation of means could be made for no juniper sites.

the organic layer and soil are integral parts of the same system, they are influenced by the same external factors. Hence, we expect similar patterns of nutrient accumulation, as observed here. However, the organic layer and soil differ in position, composition, and in chemistry among nutrients. These differences account for differences in accumulation patterns observed between the organic layer and soil, and among nutrients.

The pattern of nutrient accumulation under juniper trees was that of "islands of fertility" described earlier for a variety of tree and shrub species (Fireman and Hayward 1952, Zinke 1962, Garcia-Moya and McKell 1970, Barth 1980, Belsky et al. 1989). The large increases in mass of the organic layer and nutrients beneath canopies with juniper size is largely attributable to the effect of accumulating biomass with size (age) (Bernhard-Reversat 1982, Tiedemann and Klemmedson 2000) and slow decomposition of juniper litter. Steepness of the gradients from boles to canopy edge (60- to 120-fold greater than in intercanopy and no juniper areas), even in the smallest size class, reflects large differences in litter production and accumulation, litter quality (Kittredge 1948, Klemmedson 1992), and microclimate (radiation, temperature, moisture) of the contrasting juniper and intercanopy sagebrush/grass environments (Tiedemann and Klemmedson 1977, Belsky et al. 1989). The steep horizontal organic layer gradients reported here contrast sharply with essentially flat gradients observed for litter under mesquite (*Prosopis juliflora* (Swartz) DC) and palo verde (*Cercidium floridum* Benth.) in the Sonoran desert (Barth and Klemmedson 1978).

Decline in concentrations of N, P and S in juniper organic layers (Table 3) with distance from bole to canopy edge is likely explained by the change in litterfall composition and decomposition environment with distance to the canopy edge.

Thus, litter quality changes as the proportions of juniper and herbaceous litterfall change near the canopy edge and as the microclimate changes, thereby hastening decomposition. Spatial distribution of litterfall is a possible explanation for under-canopy nutrient gradients. Zinke (1962) reported that bark litter of several forest trees, found in rings next to boles, differed in pH and element composition from leaf litter that dominated an outer ring extending to the canopy edge. We observed no distinct accumulations of bark under junipers, but did not sort litterfall for composition. However, based on Zinke's (1962) data, we probably would have found different nutrient patterns in juniper organic layers and soils had there been a distinct zone of accumulating bark litter.

We have no explanation for the significant tree size X distance interaction displayed for C_{org} concentration in the organic layer and conclude it is an aberration in the data. That C_{org} concentration of the organic layers did not follow the pattern for N, P and S discussed above is attributed to the relative supply of these elements to decomposer organisms and their fate during early stages of decomposition. Carbon is abundant in organic layers, while N, P and S are usually limited (Swift et al. 1979). As mineralization-immobilization proceeds, excess C is evolved continuously as CO_2 while N, P, and S are retained in immobilized form.

The significant effect of distance on amounts of organic layer nutrients is a straightforward result of the distance effect on organic layer mass (Table 2) and nutrient concentration (Table 3). The change in composition of litterfall along the distance gradient has a bearing on both of these variables.

Although the horizontal pattern of soil nutrient accumulation in the juniper-intercanopy system was similar to that for the organic layer, the magnitude of distance gradients was markedly flatter. Soil nutrient concentrations ranged from 1.18- to 1.76-fold higher at tree boles than at canopy edge and intercanopy areas, except for P (1.02-fold) and Mg_{ex} (1.12-fold). In the same locale, Doescher et al. (1987) found concentrations of soil organic matter, N, Ca_{ex}, and K_{ex} under mature western juniper 1.1- to 1.6-fold higher than in the intercanopy areas. Barth (1980) found organic matter and extractable K about 3.4-fold higher, but P an unusual 20-fold higher under 490-yr-old pinyon pine (*Pinus edulis* Engelm.) than in the intercanopy areas. Tiedemann and Klemmedson (1973) reported 3.0- and 2.6-fold tree-intercanopy differences for N and S for mesquite-grass systems in Arizona.

Our findings are generally consistent with the literature regarding the mosaic pattern of nutrient distribution found in savannas, or in grasslands and shrublands invaded by trees or shrubs. However, we differ in some respects on source

of nutrient gains. Some authors (Charley and West 1975, Barth 1980, Klopatek 1987) have concluded or implied that enrichment of canopy area soils means a loss from intercanopy areas. That does not necessarily follow. In our study, all nutrients except Ca_{ex} and Mg_{ex} were enriched in soils beneath junipers. However, only Mg_{ex} and Ca_{ex}, and possibly N, displayed significant loss from the intercanopy area compared with no juniper areas. This is not to say that gains of other nutrients (C_{org}, P, S, and K_{ex}) in canopy soils did not come, in some measure, from intercanopy soils. However, other sources may have been important to canopy soil and organic layer gains of these nutrients. The question remains as to where Ca and Mg absorbed from intercanopy areas resides, since canopy soils showed no accumulation of these nutrients. Logically it appears these nutrients were absorbed and stored in the tree biomass.

Although not measured here, temperature probably contributed significantly to spatial distribution of soil and organic layer nutrients of juniper-intercanopy systems. The widely reported influence of trees and shrubs on soil and litter properties (Muller 1887, Harradine 1958, Zinke 1962, Garcia-Moya and McKell 1970) has focused chiefly on plant to soil nutrient transfers. Although the general effects of tree and shrub canopies on understory temperatures are universally understood, the spatial effects of understory temperatures on nutrient accumulation have been scarcely recognized (Tiedemann and Klemmedson 1986). Along transects from juniper boles to intercanopy areas, the state of the system (Jenny 1961) and its microenvironment changes with growth to maturity of junipers. In turn, decomposition and mineralization processes, and status of nutrients associated with litter and organic matter, change along these gradients. The role of temperature on soil and organic layer nutrient accumulation in juniper-intercanopy systems should be studied.

The juniper-sagebrush/grass system, of course, is not static. Once junipers are harvested or removed, the plant biotic factor is again changed. Nutrient availability may be improved in former juniper soils and productivity of herbaceous vegetation increased for a period of years (Thran and Everett 1987, Rose and Eddleman 1994). Following harvest of junipers, however, total soil nutrients should seek the old steady state conditions of the sagebrush/grass system, probably within a short period of time for organic-based nutrients (C_{org}, N, S, and P), based on findings of Tiedemann and Klemmedson (1986), but probably a much longer time for Ca_{ex} and Mg_{ex} (Adams and Boyle 1982).

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Biomass and Nutrient Distribution and System Nutrient Budget for Western Juniper in Central Oregon.

Abstract

Invasion of western juniper (*Juniperus occidentalis* Hook.) into big sagebrush (*Artemisia tridentata* Nutt.) communities of eastern Oregon implies redistribution of nutrients among ecosystem components, with management implications as stands mature. To assess these effects, we measured biomass and nutrients in juniper trees of five size classes ranging in average age from 36 to 161 yr, and in understory vegetation. Understory was measured at 0.0, 0.5, 1, 2, and 4 canopy radii from the bole and in areas devoid of juniper ("no juniper"). Tree size and distance from boles had no effect on biomass or concentrations and amounts of nutrients in understory vegetation. Above-ground tree biomass increased with maturity from 18.4 kg for size class 1 to 741.4 g for class 5. Biomass accumulated rapidly (22.3 kg/tree/yr) between classes 2 and 3. Foliage comprised 41% of tree biomass in class 1 trees, but decreased to 15% for class 5 trees. Concomitantly, percentage of tree biomass in boles and live branches increased from 29 to 47%. From class 1 to class 5, amounts of nutrients increased as follows: nitrogen (N) from 89 to 2117 kg/tree; phosphorus (P) from 12 to 283 g/tree; and sulfur (S) from 10 to 294 g/tree. In open systems (intercanopy and "no juniper" areas), soil contained 89.9 to 99.8% of the organic carbon (C_{org}), N, P, and S of entire systems. For tree systems (areas occupied by juniper canopies), C_{org}, N, and S in aboveground biomass increased with increasing tree maturity, while P did not change. For the most mature trees, proportions of total system N, S and P allocated to the organic layer and trees was 30, 78, and 5%, respectively. Considering the N and S limited nature of these sites, a conservative harvest management approach that emphasizes retention of organic layers and tree foliage appears prudent.

Introduction

Maintaining adequate levels of essential plant nutrients is important to productivity and stability of any plant community. In central Oregon and northern California, western juniper (*Juniperus occidentalis* Hook.) has been managed largely without regard to the consequences of management activities on nutrient status and potential site productivity. To achieve forage production, wildlife management and watershed improvement goals, juniper trees have been cut, chained, or cabled, and residues piled or windrowed and burned (Valentine 1980, Miller and Wigand 1994, Belsky 1996). Now, significant markets are emerging for western juniper for a variety of wood products (Leavengood and Swan 1998). This could eventually result in western juniper removal from several thousand ha per yr.

If western juniper functions like other shrub and tree species of arid and semi-arid regions, invasion and development to maturity may be accompanied by transfer of nutrients from intercanopy areas to tree biomass and to organic layers and soil beneath the canopies of juniper trees (Charley 1972, Tiedemann and Klemmedson 1973, Barth and Klemmedson 1978, Barth 1980, Belsky et al. 1989, Rhoades 1997). Western juniper has a wide spreading lateral root system (Young et al. 1984, Tiedemann and Klemmedson 1995) that suggests it may accumulate nutrients from intercanopy areas and sequester them in tree components. Removal of trees results in loss of nutrients from the site that may affect future productivity (Malkonen 1975, Kimmins 1977, Wells and Jorgensen 1979, Tiedemann 1987a, Everett and Thran 1992). Broadcast burning of felled trees and residues has the potential for substantial volatilization losses of some nutrients, especially nitrogen (N) and sulfur (S) (Klemmedson 1976, DeBano and Conrad 1978, Raison et al. 1985, Tiedemann 1987b). Phosphorus (P) losses from the litter may approach 50% (DeBano and Klopatek 1988). Burning piles or windrows of trees also concentrates elements such as P, calcium (Ca), potassium (K), and magnesium (Mg) beneath

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burned piles (DeBano et al. 1987). This may cause a long-term redistribution of these elements from areas occupied by trees to a relatively small portion of the total area. Increased leaching and erosion following treatment may also result in losses of essential plant nutrients (DeBano et al. 1998)

Soil-plant systems of western juniper have not been examined to determine the effect of juniper invasion into big sagebrush (*Artemisia tridentata* Nutt.) communities and development to maturity on distribution of nutrients among mineral soil, organic layers, understory vegetation, and trees of juniper/sagebrush systems. If, as juniper matures, a substantial proportion of the total nutrient capital of a site is contained in the aboveground biomass, care should be exercised to retain as much nutrient capital on the site as feasible in harvesting operations. Productivity concerns may be particularly applicable to semi-arid tree ecosystems such as western juniper (Tiedemann 1987a, Everett and Thran 1992).

The purpose of this study was to quantify accumulation patterns of biomass and nutrients in understory vegetation and trees associated with invasion and development to maturity of western juniper trees. We also compare total system nutrient accumulation patterns for "open systems" (intercanopy and areas devoid of juniper) with those for "tree systems" (areas occupied by juniper tree canopies).

The Study Area

We conducted this study in central Oregon at the Three Springs Ranch about 11 km southwest of Prineville at an elevation of 1110 m. Klemmedson and Tiedemann (2000) provide a complete description of the study area. Briefly, the study area is typical of the community dominated by western juniper on the central Oregon Plateau east of the Cascade Mountains. Climate is continental with maritime influence of storms from the Pacific coast. The area receives 26.6 cm of precipitation annually, mostly in the form of snow. Mean January and July temperatures are 0°C and 18.2°C.

Soils are young, formed in volcanic ash from eruption of Mt. Mazama 6845 ± 45 years ago (Bacon 1983). Five soil series occur in the study area: Stukel, Deschutes, Stukmond, Redmond, and Lickskillet (personal communication with Amanda Moore, Soil Scientist, United States Department of Agriculture, Natural Resources Conservation Service, Redmond, Oregon). Our study sites were primarily on Stukel series soils. These soils are well-drained, shallow (25 to 50 cm) loamy, mixed, superactive, mesic Lithic Haploxerolls (United States Department of Agriculture, Natural Resources Conservation Service 1999). Vegetation of the juniper understory, intercanopy, and areas devoid of juniper is dominated by big sagebrush, rabbitbrush (*Chrysothamnus* spp.), bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith [now *Pseudoroegneria spicata*]), and Idaho fescue (*Festuca idahoensis* Elmer).

Procedures

Site Selection and Field Sampling

We selected five separate, non-contiguous, replicate sites for sampling, all within an area 1 X 8 km. Sample sites were selected for uniformity of climate, topography (2 to 5% eastward slope), parent material, and soil. Except for an occasional tree that had been harvested for fuelwood, the area was undisturbed. Length of time the area had been excluded from grazing was not possible to determine. However, there was a well developed organic layer beneath mature trees, and no evidence of livestock disturbance or feces. This suggested that grazing had been excluded for a long time. More detailed information on site selection is provided by Klemmedson and Tiedemann (2000).

At each of the five sites, we selected three trees in each of five size classes and randomly selected one tree in each class for sampling. This resulted in a total of 25 sample trees—five replications of five size class trees (Figure 1 a–e). These are referred to as size classes 1 through 5. Size classes were subjective and based on the distribution of tree sizes on the study area. Individual sample trees were isolated from other trees by 30 to 40 m.

At each of the five sites, we selected a 5 to 10 ha area without juniper that we refer to as "no juniper." Within each "no juniper" area, three plots were established by random distance and direction from a central starting point. One plot was randomly selected from these for sampling.

Understory biomass samples were collected from a 0.5 m^2 area at the base of each sample tree (distance 0), and at 0.5, 1, 2, and 4 canopy radii due north from the bole of each tree. Biomass

Figure 1. Size distribution of typical western juniper trees used in this study. A through E = size classes 1 through 5.

samples also were collected from "no juniper" sites. Shrubs were separated into foliage and stems.

Each tree was felled (5 cm above ground level) onto large tarpaulins. Tree length was measured and all branches were removed and sorted into two categories: <3 cm and >3 cm based on expected N content. Previous laboratory study had shown that a 3 cm diameter gave the best separation of branches of low versus high N concentration. Boles were cut into 1.0 m sections; 5 cm sample slices were removed from each bole section and from >3 cm branches. Three to five branches from the <3 cm diameter category were randomly selected from each tree for determination of the proportion of biomass in categories of: foliage; live branches <0.5 cm, 0.5 to 1 cm, and 1 to 3 cm diameter; and dead branches <1 cm and >1 cm diameter. Each branch was then separated by hand into these categories. The proportion of branch weight in each category was used to determine the proportion of total branch weight <3 cm in each category. After field-weighing of all understory biomass components (grass, forb, and shrub) and all tree components, samples

of each component were collected, sealed in double plastic bags, and returned to the laboratory under refrigeration for moisture determination. Field weights of all biomass components were then corrected to oven-dry weight at 70°C. Small samples of each biomass component were collected, air-dried, and ground to 0.25 mm fineness for laboratory analysis of nutrient content.

Dr. Franco Biondi, Tree Ring Laboratory, University of Arizona, Tucson, aged each tree from a slice of the lowermost bole section. Roots of trees and understory vegetation were not collected. Although this omission underestimates the amount of nutrients incorporated into biomass, measuring this biomass component was beyond the objectives of the experiment.

Chemical Analyses

Understory vegetation and tree components were analyzed for total organic C by dry combustion using a high-frequency induction furnace (Nelson and Sommers 1982), total N by the micro-Kjeldahl procedure (Bremner and Mulvaney 1982), total P by dry ashing in the presence of magnesium nitrate followed by vanadate-molybdate yellow color development (Chapman and Pratt 1961), and total S by dry combustion in a high-frequency induction furnace (Tiedemann and Anderson 1971). Nutrient concentrations of bole sections were averaged for statistical analyses.

Statistical Analyses

Data for understory biomass and contained nutrients (concentrations and amounts) were analyzed as a randomized complete block with sites as blocks and size class (including "no juniper") and distances as main effects [SAS Institute Inc. (1987) analysis of variance]. Biomass, concentrations of nutrients, and nutrient amounts by tree component were analyzed as a randomized complete block with sites as blocks and size class as the main effect. Tree component was treated as a split-plot. The LSD test ($P \leq 0.05$) was used for determination of differences among means for main effects, split-plot effects, and interactions significant at $P \leq 0.05$ (Carmer and Swanson 1971).

Development of a Complete System Nutrient Budget

Biomass and nutrient accumulation data were expressed on a kg/m^2 or g/m^2 basis for mineral soil, organic layers, understory vegetation, and trees for open systems (intercanopy and "no juniper" areas) and for tree systems (areas occupied by juniper canopies). For tree systems, nutrient accumulation is expressed on the basis of crown occupancy area. Organic layer and soil data are from Klemmedson and Tiedemann (2000). Weighted average values for the organic layer and soil for each tree were determined from amounts of nutrients calculated for three concentric bands (each one-third canopy radius in width) from nutrient data for the 0, 0.5, and 1 canopy radii locations representing inner to outer bands, respectively. Data for the three bands were then summed and divided by canopy area to obtain g/m^2 values for each nutrient, for each tree size class. No statistical analyses were performed on nutrient budget values.

Results and Discussion

Biomass and Concentrations and Amounts of Nutrients in Understory

Biomass, nutrient concentrations, and amounts of nutrients in understory vegetation were unaffected by size class (including "no juniper"), distance from tree boles, and the size class X distance interaction. Biomass of understory vegetation averaged 163 g/m^2 (1630 kg/ha). Concentrations of C_{org}, N, P, and S in understory vegetation averaged 425, 8.2, 1.3, and 1.0 g/kg; amounts of C_{org}, N, P, and S in understory averaged 69.8, 1.12, 0.20, and 0.15 g/m^2, respectively.

Lack of differences in biomass of understory vegetation between areas under tree canopies, intercanopy, and areas without juniper was contrary to observations of other semi-arid woodlands (Clary and Morrison 1973, Bedell and Bunch 1978, Tiedemann and Klemmedson 1977, Belsky et al. 1989, Belsky 1994). Understory biomass has generally been shown to be greater beneath canopies of trees than in adjacent openings. In some cases, differences between these locations were primarily the result of higher cover and production of perennial grasses under tree canopies (Clary and Morrison 1973, Tiedemann and Klemmedson 1977). We did not measure differences in plant composition between canopy and intercanopy areas.

Physical Characteristics of Sample Trees

Average tree age ranged from 36 yr for class 1 to 161 yr for class 5 (Table 1). The youngest tree was 21 yr; the oldest 231 yr. Average height among

TABLE 1. Ages and physical characteristics of five size classes of western juniper trees sampled in this study.

Size Class	Age (yr)		Height (m)		Basal Diameter (cm)		Canopy Diameter (m)	
	Ave.	Range	Ave.	Range	Ave.	Range	Ave.	Range
1	36	21-58	3.3	2.9-3.8	13	11-17	1.7	1.6-2.2
2	55	37-68	4.8	4.1-6.0	22	17-26	2.5	2.1-3.3
3	62	41-85	7.0	5.7-8.2	37	29-43	4.5	3.2-5.6
4	101	44-154	9.5	8.5-11.7	49	44-53	6.3	5.3-8.7
5	161	108-231	9.9	9.2-10.4	63	58-68	6.7	5.6-7.8

TABLE 2. Distribution of biomass (kg) among tree components.

Size Class	Component								Total
	Boles	Foliage	Live Branches				Dead Branches		
			>3 cm	1-3 cm	0.5-1 cm	<0.5 cm	>1 cm	<1 cm	
1	4.7[a1]	7.6[a]	0	3.5[a]	0.8[a]	0.9[a]	<0.1[a]	0.1[a]	18.4[a]
2	15.4[a]	19.3[a]	0	14.8[a]	2.3[a]	2.8[a]	<0.1[a]	0.2[a]	56.4[a]
3	55.5[b]	50.2[b]	20.9[a]	55.5[b]	7.7[a]	6.6[a]	3.8[a]	1.3[a]	212.3[b]
4	146.6[c]	91.4[c]	71.9[b]	86.2[c]	12.9[a]	15.0[a]	8.9[a]	2.1[a]	433.6[c]
5	238.5[d]	113.9[c]	130.1[c]	156.5[d]	18.3[a]	20.8[a]	14.7[a]	5.2[a]	741.4[d]

[1] Values in a column with the same lower case letter are not significantly different at $P \leq 0.05$.

classes ranged from 3.3 to 9.9 m but overall height (irrespective of size class) ranged from 2.9 to 10.4 m. Basal diameter for class 1 averaged 13 cm, which for size class 5 was nearly 5 times greater (63 cm). Canopy diameters ranged from 1.7 m to 6.7 m.

Biomass of Trees and Tree Components

Tree biomass increased markedly with size class from 18.4 kg for class 1 to 741.1 kg for class 5 (Table 2); differences among larger classes (2 - 5) were all significant.

Because the size class X tree component interaction for biomass was highly significant, we focus here on explaining the interaction, and note differences among size classes for individual components. These comparisons relate directly to study objectives. Biomass of boles, foliage, and live branches >3 cm and 1 to 3 cm diameter increased significantly with size class. By contrast, tree size had no influence on smaller live branches (<1 cm) or dead branches, hence the significant interaction (Table 2). For classes 1 and 2, foliage comprised the greatest part of the tree biomass (41.3 and 34.2%). Foliage, boles, and live branches 1 to 3 cm diameter, were roughly equal in biomass for class 3. As trees matured (class 5), boles, live branches 1 to 3 cm diameter, and live branches >3 cm diameter became the major tree components.

Figure 2 portrays the percentage of tree biomass in each tree component for each size class. The most striking change with increasing tree maturity was for foliage. Between class 1 and 5, percentage of total tree biomass in foliage declined from 41 to 15. This was not unexpected; Rodin and Bazilevich (1967) reported that young trees generally have a greater proportion of biomass allocated to foliage than mature trees. Foliage biomass, as a proportion of tree biomass, however, was comparable to that measured by Gholz (1980) for western juniper (20%) and for 90- and 350-year old one-seeded juniper (*Juniperus monosperma* Sarg.) in northern Arizona (22% and 12%, respectively) determined by Grier et al. (1992). However, the high mean percentage of biomass in foliage (26%) and the high proportion of foliage in mature junipers (15% for class 5) was substantially greater than that (3 to 9%) normally allocated to foliage in conifers (Rodin and Bazilevich (1967).

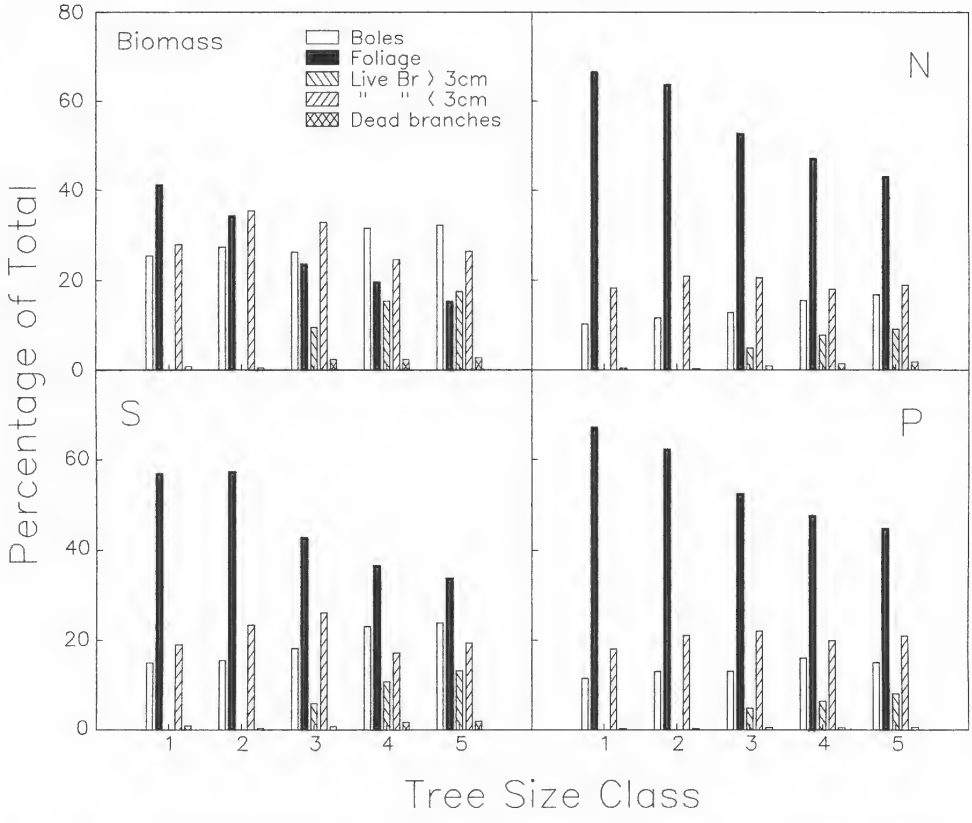

Figure 2. Percentage distribution of tree biomass, N, S, and P among tree components for five size classes of western juniper.

Large live branches (>3 cm diameter) was the only other tree component that changed markedly with increasing tree size, from 0 to 17% between class 2 and 5 (Figure 2). Changes in proportions of other tree components among classes were minor.

Live and dead branches were important components of western juniper; they comprised 29 to 47% of tree biomass. This is not unusual for juniper. Gholz (1980) found that live and dead branch biomass comprised 38% of tree biomass in western juniper. Grier et al. (1992) reported that branches comprised 57 to 62% of tree biomass for 90- and 350-year old one-seeded juniper in northern Arizona.

The highest rate of tree biomass accumulation (22.3 kg/tree/year) occurred between classes 2 and 3, an interval of 7 years (Table 3). Yearly increment patterns indicate that the growth pattern of

TABLE 3. Annual rates of accumulation of biomass and nutrients in western juniper as a function of tree size class.

Size Class	Elapsed Years	Biomass (kg/yr)	N (g/yr)	P (g/yr)	S (g/yr)
1	36	0.5	2.5	0.3	0.3
2	19	2.0	7.3	1.0	0.8
3	7	22.3	69.7	9.4	10.6
4	39	5.7	17.7	2.5	2.3
5	60	5.1	11.8	1.4	1.7

TABLE 4. Concentrations of nutrients (g/kg) in tree components of western juniper (average of size classes).

Tree Component	Nutrient			
	C_{ORG}	N	P	S
Foliage	505[c1]	7.67[e]	1.06[d]	0.80[c]
Live Branches <0.5 cm	476[a]	3.76[d]	0.53[c]	0.42[b]
Live Branches 0.5-1 cm	480[ab]	2.88[c]	0.40[c]	0.35[a]
Live Branches 1-3 cm	489[b]	2.18[b]	0.30[b]	0.33[a]
Live Branches >3 cm	491[2]	1.51	0.19	0.28
Boles	488[b]	1.80[a]	0.27[b]	0.32[a]
Dead Branches <1 cm	483[ab]	2.81[c]	0.28[b]	0.40[ab]
Dead Branches >1 cm	481[ab]	2.09[b]	0.13[a]	0.33[a]

[1] Values in a column with the same lower case letter are not significantly different at $P \leq 0.05$.
[2] No LSD test for this category because there were no samples for Size Classes 1 and 2.

western juniper trees followed an S-shaped growth curve, confirming results of Eddleman (1987).

Nutrient Concentrations in Tree Components

Concentrations of N, P, and S (averaged among tree size classes) were greater ($P \leq 0.05$) in foliage than in other tree components (Table 4) and declined to low levels in dead branches and boles. Although concentration of C_{org} was highest in foliage, it varied little among components.

Concentration of N in foliage of western juniper trees (average 7.7 g/kg) was near the lower end of the range for coniferous forests worldwide (Rodin and Bazilevich 1967), whereas concentrations of P and S were in the middle of the range.

Accumulation of Nutrients in Tree Components

Accumulation of nutrients for individual tree components was directly related to accumulation of biomass, i.e., increase in tree size (Table 5). This was especially so for C_{org}, where the correspondence between C_{org} and biomass was near 1:1, i.e., concentration of C_{org} varies <3% among tree components (Table 4). For that reason, we have not included data for C_{org} in Table 5. The analysis of variance showed that the interaction of size class X tree component significantly ($P \leq 0.0001$) influenced amounts of C_{org}, N, P, and S. Two factors appear responsible for the significant interaction. First, there were no live branches >3 cm diameter for classes 1 and 2 (Table 5). Secondly, accumulation of C_{org}, N, P, and S among size classes was much greater for boles, foliage, and live

TABLE 5. Distribution of nutrients (g) among tree components by tree size class.

Nutrient	Size Class	Tree component								Total
		Boles	Foliage	Live Branches				Dead Branches		
				>3 cm	1-3 cm	0.5-1 cm	<0.5 cm	>1 cm	<1 cm	
Nitrogen	1	9.1[a]	59.4[a]	0	9.6[a]	2.8[a]	3.9[a]	<0.1[a]	0.4[a]	89.4[a]
	2	26.3[a]	145.1[a]	0	30.0[a]	6.6[a]	10.8[ab]	0.1[ab]	0.6[a]	228.0[a]
	3	89.9[b]	375.4[b]	34.1[a]	101.2[bc]	20.9[bc]	24.6[b]	4.2[bc]	2.4[a]	715.8[b]
	4	217.1[c]	661.4[c]	109.0[a]	173.5[c]	30.9[c]	49.1[c]	16.9[c]	3.5[a]	1408.4[c]
	5	355.0[d]	906.1[d]	193.6[b]	287.9[d]	42.9[d]	70.1[d]	30.4[d]	8.6[b]	2116.8[d]
Phosphorus	1	1.4[a]	8.2[a]	0	1.3[a]	0.4[a]	0.5[a]	0	<0.1[a]	12.2[a]
	2	4.0[a]	19.2[a]	0	4.0[a]	1.0[ab]	1.5[ab]	0	0.1[a]	30.8[a]
	3	12.6[b]	50.7[b]	4.6[a]	14.9[ab]	3.0[bc]	3.6[b]	0.3[a]	0.3[a]	96.8[b]
	4	31.2[c]	92.1[c]	12.4[ab]	26.4[bc]	4.4[cd]	7.6[c]	0.6[a]	0.3[a]	193.3[c]
	5	42.9[d]	127.0[d]	23.0[b]	41.8[c]	6.1[d]	11.3[d]	1.9[b]	1.2[b]	283.5[d]
Sulfur	1	1.5[a]	5.7[a]	0	1.4[a]	0.4[a]	0.4[a]	0	0.1[a]	10.0[a]
	2	4.1[a]	15.2[ab]	0	4.2[ab]	0.9[a]	1.1[a]	0	0.1[a]	26.5[a]
	3	18.4[b]	43.2[bc]	5.9[a]	21.0[b]	2.3[b]	3.0[ab]	0.5[a]	0.3[a]	100.7[b]
	4	44.0[c]	69.8[cd]	20.3[ab]	22.4[b]	5.1[cd]	5.5[b]	2.7[ab]	0.7[ab]	190.6[c]
	5	70.2[d]	99.7[d]	38.9[b]	43.6[c]	4.7[d]	8.8[c]	4.8[b]	1.3[b]	294.2[d]

[1] Values in a column with the same lower case letter are not significantly different at $P \leq 0.05$.
[2] Total tree values do not equal the sum of individual components because the "debris" category is not shown in the table.

branches 1 to 3 cm diameter than for the other components.

As implied above, tree amounts of C_{org} increased in parallel fashion to biomass (Table 2), from 9 kg for class 1 to 368 kg for class 5. Tree N increased from 89 to 2117 g between classes 1 and 5. Although amounts of P and S accumulated were about one-tenth the amount of N, rates of increase between classes 1 and 5 were similar to those for N. Tree accumulations of C_{org}, N, P, and S were not significantly different for classes 1 and 2, but these two classes differed significantly from all larger size classes, and they from each other (Table 5).

Nutrient accumulation proceeded slowly for all tree components for young trees (classes 1 and 2), but accelerated as trees increased in size and accumulated biomass. Nutrient accumulation among size classes was most pronounced in boles, foliage, and live branches 1 to 3 cm and 0.5 to 1 cm diameter (Table 5). For these components (with exception of S in live branches 1 to 3 cm diameter), nutrient amounts were significantly greater in classes 4 and 5 than in classes 1 and 2. The other consistent aspect of the data for all nutrients and tree components was significantly greater nutrient amounts for class 5 than for class 3.

Annual rates of accumulation of biomass and all nutrients increased with tree size, reaching a maximum in class 3, then declined with maturity in classes 4 and 5 (Table 3),

Foliage was the predominant component home for N, P, and S in western juniper throughout the life of the trees (Figure 2). However, as size (age) increased, the percentage of each of these nutrients residing in foliage declined, reaching a minimum of about 43-45% of the tree total for N and P, and 34% for S. Concurrently, the relative amount of N and S increased slightly in boles and live branches >3 cm diameter. Live branches <3 cm diameter were the second most important component for accumulation of N, P, and S in western juniper, containing about 20% of the total.

Nutrient Budget for Soil, Organic Layer, Understory, and Trees

Nutrient Accumulation Patterns in Open Systems

Accumulations of C_{org}, N, P, and S in soil, organic layer, and understory vegetation were similar at intercanopy distances 2 and 4 for all size classes (Klemmedson and Tiedemann 2000). In the organic layer, amounts of N for "no juniper" sites tended to be lower, but not significantly so, than that for intercanopy locations. Amounts of C_{org}, P, and S in the organic layer did not differ among "no juniper" and intercanopy locations.

We were unable to make statistical comparisons of mineral soil among intercanopy and "no juniper" areas because of the unbalanced experimental design. However, amounts of C_{org}, N, P, and S in soil for "no juniper" areas were within the range of values for intercanopy distances 2 and 4 and, hence, would not likely have differed significantly (Klemmedson and Tiedemann 2000). Total accumulations of C_{org}, N, P, and S in open systems were 2176, 243.9, 228.5, and 4.1 g/m^2, respectively (Table 6). Most (89.9 to 99.8%) of the C_{org}, N, P, and S in these systems was contained in the soil. Aboveground amounts of these nutrients in open systems were about equally allocated between the organic layer and understory vegetation.

Nutrient Accumulation Patterns in Tree Systems

The largest proportion of total system C_{org} (61 to 69%) was contained in trees (Table 6). Between classes 1 and 5, C_{org} increased 2.4 times, i.e., at the same rate as biomass. In the organic layer, C_{org} increased five-fold between classes 1 and 5; i.e., from 303 to 1503 g/m^2 of system C_{org}. While C_{org} increased from 2125 to 2697 g/m^2 in the mineral soil between classes 1 and 5, the percentage of total system C_{org} declined from 33 to 20% (Table 6).

Most of the N in this system (70 to 84%) was contained in mineral soil. Amounts of soil N increased with increasing tree size, but the proportion contained in the soil declined from 84 to 70% from class 1 to 5. The most salient result of the N budget was that by the time trees reached maturity (class 5), 30% of N was contained in trees and organic layers.

Phosphorus resided primarily in the mineral soil and the proportional distribution (95 to 97%) did not change with tree size (Table 6). By contrast, P accumulation (g/m^2) in the organic layer increased 6-fold from class 1 to 5 (Table 6). Most of the aboveground P was contained in tree biomass, but amounts accumulated were similar, regardless of tree size, except for the largest trees.

TABLE 6. Distribution of carbon, nitrogen, phosphorus, and sulfur in open-intercanopy and western juniper systems as a function of tree size class.

Nutrient	Tree Size Class[1]	System Component								Total	
		Trees		Understory		Organic Layer		Mineral Soil			
		g/m²	%	g/m²	%	g/m²	%	g/m²	%	g/m²	%
Carbon	Open	0	0	96	4.4	93	4.3	1987	91.3	2176	100.0
	1	3882	61.0	49	0.8	303	4.8	2125	33.4	6359	100.0
	2	5263	62.1	45	0.5	634	7.5	2537	29.9	8479	100.0
	3	6310	69.1	71	0.8	753	8.2	1994	21.8	9128	100.0
	4	6938	63.5	46	0.4	1199	11.0	2736	25.1	10919	100.0
	5	9390	68.9	32	0.2	1503	11.0	2697	19.8	13622	100.0
Nitrogen	Open	0.0	0.0	1.58	0.7	2.26	0.9	240	98.4	243.9	100.0
	1	38.5	13.3	0.90	0.3	8.05	2.8	243	83.7	290.5	100.0
	2	43.8	13.2	0.50	0.2	20.23	6.1	268	80.6	332.5	100.0
	3	43.5	14.3	1.10	0.4	23.81	7.8	236	77.5	304.4	100.0
	4	42.9	12.1	0.80	0.2	31.18	8.8	280	78.9	354.9	100.0
	5	59.8	16.2	0.50	0.1	49.82	13.5	258	70.1	368.1	100.0
Phos-	Open	0.0	0.0	0.31	0.1	0.22	0.1	228	99.8	228.5	100.0
phorus	1	5.2	2.3	0.12	0.1	0.71	0.3	224	97.4	230.0	100.0
	2	5.7	2.4	0.09	<0.1	1.34	0.6	226	96.9	233.1	100.0
	3	5.9	2.6	0.14	0.1	1.88	0.8	220	96.5	227.9	100.0
	4	5.9	2.5	0.10	<0.1	2.36	1.0	230	96.5	238.4	100.0
	5	8.0	3.4	0.08	<0.1	4.16	1.8	225	94.8	237.2	100.0
Sulfur	Open	0.0	0.0	0.20	4.9	0.21	5.2	3.66	89.9	4.1	100.0
	1	4.2	47.2	0.12	1.3	0.94	10.6	3.63	40.8	8.9	100.0
	2	5.1	46.7	0.10	0.9	1.91	17.5	3.82	34.9	10.9	100.0
	3	6.1	50.2	0.14	1.2	2.42	19.9	3.48	28.7	12.1	100.0
	4	5.7	45.0	0.10	0.8	2.82	22.2	4.06	32.0	12.7	100.0
	5	8.3	47.9	0.08	0.5	5.14	29.7	3.79	21.9	17.3	100.0

[1] Values shown for "open" are the average of values for "no juniper" and intercanopy sites (distances 2 and 4 for tree size classes 1-5)

The pattern of S distribution among ecosystem components and size classes differed distinctly from that of N and P in most respects. Most of the S (59 to 78%) was in trees and the organic layer, with the largest amount in trees. Although the amount of S in trees almost doubled between classes 1 and 5, the proportion of system total remained fairly constant (45 to 50%). Most of the distributional difference of S among classes occurred in the organic layer, as in the case of P; the amount of S increased 5-fold from class 1 to 5 while proportion of total system S increased 3-fold. Amounts of soil S were relatively constant among classes (3.5 to 4.1 g/m²), but the proportion of total declined from 41 to 22% between class 1 and 5 (Table 6).

Results of Everett and Thran (1992), who looked at nutrient distribution in entire stands of singleleaf pinyon (*Pinus monophylla* Torr. & Frem.) in Nevada, are not directly comparable with this study, but nonetheless worth noting. They found 53% of the site N incorporated in trees and organic layers, about three-fourths of which was in the organic layer. Our oldest trees had 30% of the system N incorporated about equally in trees and organic layers. Although P was stored primarily in soil in both western juniper and singleleaf pinyon systems, the difference in distribution (96% versus 85%) is noteworthy. Sulfur distribution presented a major contrast between the two studies. We found 59 to 78% of S in aboveground components compared to only 13% in singleleaf pinyon tree systems (Everett and Thran 1992).

Comparisons of Open and Tree Systems

Comparing storage of C_{org}, N, P, and S in open systems with that in the tree system reveals much about change in nutrient status of this sagebrush/

grass system as western juniper invades and grows to maturity. Even for the youngest trees, the amount of C_{org} in the tree system was three times greater than that of open systems. For class 5, this difference was more than 6-fold. Even the smallest (youngest) tree system (class 1) contained 16% (47 g/m^2) more N than the open systems. Class 5 had accumulated 51% more N (124 g/m^2) than open systems.

System P, in contrast to N, was reasonably comparable between open and tree systems. However, S accumulation differed more between tree and open systems than N. Amount of S accumulated in the tree system was 2- to 4-fold greater than open systems, depending on tree size.

Comparisons of tree with open systems indicate that western juniper effectively accumulates C_{org}, N, and S. Lack of noticeable accumulation of P by juniper systems may be due to the high soil P status prior to juniper invasion. Sources of N and S accrued to the tree system were not ascertained, but these additions apparently were not at the expense of intercanopy soils. Several sources, both biotic and abiotic, could account for net accrual of these nutrients to tree systems without a significant loss from intercanopy areas. These sources of nutrient accrual to "fertile islands" are described in the introduction to the companion paper (Klemmedson and Tiedemann 2000).

As the state of the system changes with growth to maturity of junipers, cooler understory temperatures and a moister microenvironment (Tiedemann and Klemmedson 1977) will promote higher steady state levels of soil organic matter and associated nutrients (Jenny 1930, Tiedemann and Klemmedson 1986). These conditions should lead to improved decomposition and mineralization, lower losses of soil C and N by volatilization and denitrification (West 1981, 1991) and more efficient cycling of nutrients in the juniper system than in the sparse vegetation of open systems (Odum 1969).

Conclusions

Biomass of juniper understory (1630 kg/ha) reflected the sparse appearance of this western juniper/big sagebrush/bluebunch wheatgrass ecosystem. As a consequence, understory vegetation was also a minor compartment of the soil/plant system for accumulation of nutrients.

Salient features of biomass distribution among tree components were: the decline in percentage of biomass in foliage (41 to 15%) with increasing tree size from class 1 to 5, the high mean percentage of biomass allocated to foliage (26%), and the high proportion of tree biomass allocated to live and dead branches 29 to 47%. Miller et al. (1990) noted high biomass allocation to foliage in young western juniper (<40 yr) and concluded this enabled western juniper to optimize photosynthetic capacity. Our observations suggest that this adaptive feature also may be important to mature trees in these warm, semi-arid environments.

Comparisons of tree and open systems indicate that western juniper plays a dominant role in capture and retention of nutrients in these semi-arid habitats. This role of juniper appears directly related to the time of occupancy. Nutrient accumulation patterns that we document for western juniper reinforces the importance Romney et al. (1978) ascribe to shrubs in desert ecosystems. They suggest that if fertile islands created by shrubs did not exist, fertility present in them would be dispersed over the entire area. For plants not capable of N-fixation, deficiency for that element would be present over the entire area.

Results of comparisons made here do not lead directly to answers to questions about effects of management of western juniper on future site productivity. Nonetheless, our results signal caution in the way western juniper is managed that will help avoid degradation of productivity. At these sites, availability of soil N and S are inherently low (Tiedemann and Klemmedson 1995) and levels of total N and S are below the range for interior Pacific Northwest volcanic ash soils (Tiedemann and Klock 1977, Geist and Strickler 1978). Even for the nutrient enriched tree system, levels of N and S are still at the low end of the range for interior Pacific Northwest volcanic soils. In tree systems, 59 to 78% of system S and 16 to 30% of system N are incorporated into organic layer and tree components. This, coupled with the nutrient-limited status of soils of these western juniper systems, suggests that retention of as much of the accumulated aboveground nutrient capital as possible is a prudent management strategy. Retention of tree foliage (i.e., lop and scatter) and the organic layer would be particularly important. An error on the conservative side can be corrected in the future. If residues and the organic layer are burned, only time can compensate

for volatilization loss of nutrients and for associated effects on productivity. West's (1991) review and results from Everett and Thran (1992) support this conclusion. West indicates that in habitats where shrubs or small trees contain a substantial part of the nutrient pool, fire may be more disruptive to nutrient cycles than livestock grazing. Further, West (1991) states that savannas and shrub-steppes "need careful management to maintain them since it is very difficult to re-establish the original structure once they are degraded."

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Diet of First-Feeding Larval and Young-of-the-Year White Sturgeon in the Lower Columbia River

Abstract

In some Snake and Columbia River reservoirs, adult white sturgeon (*Acipenser transmontanus*) are common but few juvenile fish are found, indicating a lack of spawning success or poor survival of larvae. In contrast, recruitment of young-of-the-year white sturgeon to juvenile and adult stages is successful in the unimpounded Columbia River downstream of Bonneville Dam. The availability and size of preferred prey during the period when white sturgeon larvae begin exogenous feeding could be an important determinant of year-class strength. To explore this issue, we examined the diet composition of 352 larval and young-of-the year white sturgeon collected from 1989 through 1991 in the lower Columbia River. Samples were collected downstream from Bonneville Dam and upstream from the dam in Bonneville and The Dalles Reservoirs. Fish that ranged in size from 15 to 290 mm in total length fed primarily on gammarid amphipods (*Corophium* spp.) during all months. This diet item became increasingly important to all sizes of white sturgeon examined as they grew. The length of *Corophium* spp. eaten by larval and young-of-the-year white sturgeon increased with increasing fish length ($r^2 = 45.6\%$, $P < 0.0001$). Copepods (Cyclopoida), Ceratopogonidae larvae, and Diptera pupae and larvae (primarily chironomids) were also consumed, especially at the onset of exogenous feeding. A small percentage of white sturgeon were found with empty stomachs during June (1.6% downstream from Bonneville Dam) and July (4.5% downstream and 2.6% in the reservoirs). Diets of larval and young-of-the year white sturgeon from both impounded and free-flowing sections of the Columbia River were similar and we found no evidence of larval starvation in the areas investigated, areas currently supporting healthy white sturgeon populations.

Introduction

Construction of dams along the Columbia and Snake Rivers has fragmented populations of white sturgeon, *Acipenser transmontanus*. The population of white sturgeon in the unimpounded Columbia River downstream from Bonneville Dam is currently robust and supports substantial sport and commercial fisheries (DeVore et al. 1995). However, upstream from Bonneville Dam population levels vary, with some reservoirs supporting relatively large populations and others having very few white sturgeon (Cochnauer et al. 1985, Beamesderfer et al. 1995, Anders and Richards 1996). In some reservoirs, adult white sturgeon are common but few juvenile fish are found, indicating a lack of spawning success or poor survival of larvae (Cochnauer et al. 1985, Beamesderfer et al. 1995). In the three reservoirs above Bonneville Dam, successive year-class failures and poor recruitment to young-of-the-year have been found (Parsley and Beckman 1994).

For many fish species, year-class strength is largely dependent on larval survival (Houde 1987, Miller et al. 1988). The two major causes of larval mortality in nature are starvation and predation, and these are most likely interrelated (Hunter 1981, Houde 1987). The availability and size of preferred prey at the onset of exogenous feeding could be an important determinant of white sturgeon year-class strength in the Columbia River. If insufficient adequately-sized prey are available, growth rates would be reduced and mortality would be increased due to greater vulnerability to predation and starvation. The objective of our study was to describe the diet composition of exogenously feeding white sturgeon larvae and young-of-the-year collected downstream from Bonneville Dam and those collected upstream in the reservoirs created by Bonneville and The Dalles Dams.

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Methods

Fish Collection

All larval and young-of-the-year (YOY) white sturgeon examined in this study were captured with trawls fished on the bottom. In the unimpounded reach downstream from Bonneville Dam (Figure 1), the National Marine Fisheries Service fished a 3.0-m beam trawl or a 7.9-m semiballoon shrimp trawl from late June through October 1990, and from late June through September 1991 (McCabe and Tracy 1994). In Bonneville and The Dalles Reservoirs, U.S. Fish and Wildlife Service (now the U.S. Geological Survey) fished either a 6.9-m high-rise trawl or a 3.0-m beam trawl to capture larval and YOY white sturgeon from July through October 1989 and 1990 (Parsley et al. 1993). The trawls were towed upstream along the bottom, for 2 to 20 minutes per set for the beam trawl and 5 to 15 minutes for the shrimp and high-rise trawls. Information on abundances of collected white sturgeon eggs, larvae, and juveniles, and their relation to water depth, flow, substrate type, and other factors are reported by McCabe and Tracy (1994) and Parsley et al. (1993).

White sturgeon larvae were collected downstream from Bonneville Dam from River Kilometer (RKm) 45 to 232 from May through late July, a distribution that suggested wide dispersal after hatching (McCabe and Tracy 1994). Young-of-the-year white sturgeon were collected from June through October downstream from Bonneville Dam between RKm 45 and 211 (Figure 1). Upstream from Bonneville Dam (RKm 234), young-of-the-year were collected from July through October from RKm 242 in Bonneville Reservoir to RKm 343 in The Dalles Reservoir.

Stomach Analysis

Larval and YOY white sturgeon were measured (total length) in the field, placed in a 4% buffered formaldehyde solution, and later transferred to vials containing 70% ethanol for storage. After weighing each fish, we removed its stomach surgically and examined the contents using a 10X binocular dissecting microscope. Food items were identified to the lowest practical taxon (usually species), but grouped at a higher taxonomic level for analysis. The percent frequency of occurrence and percent numbers of each food category were

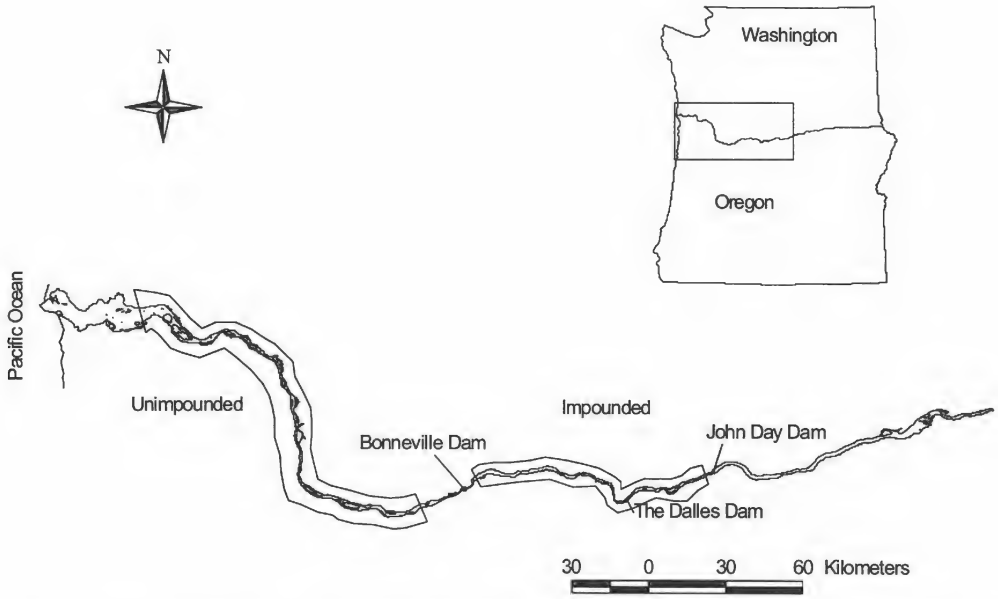

Figure 1. Lower Columbia River showing approximate locations where larval and young-of-the-year white sturgeon were captured for food habits analysis from 1989 through 1991.

then calculated. Weights of individual food items were not taken because of their small sizes. Data were stratified by month (with September and October combined) and by area (upstream and downstream from Bonneville Dam).

Corophium spp. (gammarid amphipods) found in stomachs of fish captured downstream from Bonneville Dam were measured to the nearest 0.1 mm (excluding antennae) using a lens micrometer, and a mean length of *Corophium* spp. consumed was calculated for each fish. The relationship between fish length and *Corophium* spp. length was then explored using linear regression.

A mean stomach fullness value (Terry 1977) ranging from one (empty) to seven (distended) was calculated for each month. Although subjective, this measure provided a useful, qualitative indication of feeding success.

Results

A total of 352 larval and YOY white sturgeon stomachs were examined; 203 from fish captured downstream from Bonneville Dam, and 149 from fish captured in Bonneville and The Dalles Reservoirs (Table 1). There was little difference in diet between years, so the years were combined for this analysis. Since few fish were sampled from The Dalles Reservoir (11) and their diet was similar to those from Bonneville Reservoir, the data from the two reservoirs were also combined. Fish ranged in size from 15 to 290 mm in length, with the average length increasing each month. During June, 20.3% of the fish sampled downstream from Bonneville Dam contained some yolk, a proportion that declined to 8% during July (Table 2). Empty stomachs were found in 1.6% (1) of the fish examined during June and 4.5% (4) during July (Table 2). No yolk sacs or empty stomachs were found in fish collected from August through October downstream from Bonneville Dam. In Bonneville and The Dalles Reservoirs, no fish were sampled in June and no fish with yolk sacs were sampled during any month (Table 3). Empty stomachs were found in 2.6% (1) of the fish sampled during July in these reservoirs, while no empty stomachs were found from August through October.

The shortest larval white sturgeon exhibiting exogenous feeding in this study were 21 mm in length. One 21-mm fish captured downstream from Bonneville Dam contained yolk material and exogenous food. The smallest fish containing exogenous food and no yolk was also 21 mm in length. Fish still containing yolk material ranged from 15 to 22 mm in length. All larvae found with empty stomachs and no yolk ranged from 20 to 22 mm in length. No empty stomachs were found in fish > 22 mm in length.

First-feeding white sturgeon (those captured during June and July) consumed *Corophium* spp., copepods (Cyclopoida), Ceratopogonidae larvae, and Diptera pupae and larvae (primarily chironomids). Other food items were eaten, but less frequently (Tables 2 and 3). *Corophium* spp.

TABLE 1. Lengths and weights of larval and young-of-the-year white sturgeon sampled each month from 1989 through 1991 in the Columbia River. Stomach fullness values ranged from one (empty) to seven (distended). Standard errors are in parentheses.

Month	N	Mean Length (mm)	Mean weight (g)	Mean stomach fullness
		Downstream from Bonneville Dam		
June	64	25.9 (0.77)	0.1 (0.01)	4.1
July	88	38.7 (2.28)	4.6 (4.05)	4.6
August	31	115.8 (6.12)	7.3 (1.15)	5.1
Sept/Oct	20	208.7 (12.11)	37.8 (4.61)	4.6
Overall	203	63.2 (4.37)	6.9 (1.96)	4.5
		Upstream from Bonneville Dam		
July	38	51.7 (3.50)	1.2 (0.21)	5.3
August	76	103.6 (3.79)	7.3 (0.84)	5.4
Sept/Oct	35	181.8 (7.46)	34.6 (4.59)	5.4
Overall	149	108.8 (4.65)	12.1 (1.55)	5.4

TABLE 2. Food habits of larval and young-of-the-year white sturgeon (by month) collected from the Columbia River downstream from Bonneville Dam, 1990 and 1991.

	June n = 64		July n = 88		August n = 31		Sept/October n = 20		Overall n =203	
Food type	Number (%)	Frequency* (%)	Number (%)	Frequency (%)	Number (%)	Frequency (%)	Number (%)	Frequency (%)	Number (%)	Frequency (%)
Oligochaeta							<0.1	5.0	<0.1	0.6
Bivalvia	0.7	4.0			<0.1	3.2	0.3	35.0	0.2	5.6
Ostracoda			0.5	2.6			0.2	20.0	0.2	3.4
Neomysis mercedis	0.2	2.0	1.3	16.9	4.5	58.1	0.5	45.0	1.9	23.0
Ramellogammarus spp.	1.2	10.0	0.3	6.5	0.2	12.9	0.1	20.0	0.3	10.1
Corophium spp.	45.2	68.0	57.2	83.1	87.2	100.0	96.8	100.0	83.1	83.7
Daphnia spp.			0.2	2.6	0.3	9.7			0.1	2.8
Cyclopoida	31.0	30.0	17.2	24.7	0.7	9.7			5.4	20.8
Ceratopogonidae larvae	7.7	22.0	14.9	53.2	2.1	51.6	0.2	30.0	4.1	41.0
Diptera larvae and pupae	13.6	52.0	8.4	68.8	4.9	77.4	1.7	55.0	4.7	65.2
Ephemeroptera	0.2	2.0			<0.1	3.2			<0.1	1.1
Isopoda							<0.1	10.0	<0.1	1.1
Hemiptera							<0.1	5.0	<0.1	0.6
Empty stomachs	1.6		4.5		0.0		0.0		2.5	
With yolk sac	20.3		8.0		0.0		0.0		9.8	

* Frequency of occurrence

TABLE 3. Food habits of young-of-the-year white sturgeon (by month) collected from the Columbia River upstream from Bonneville Dam, 1989 through 1991.

	July n = 38		August n = 76		Sept/October n = 35		Overall n = 149	
Food Type	Number (%)	Frequency* (%)	Number (%)	Frequency (%)	Number (%)	Frequency (%)	Number (%)	Frequency (%)
Oligochaeta					<0.1	2.9	<0.1	0.7
Bivalvia					0.2	14.3	0.1	3.4
Neomysis mercedis	3.8	29.7	2.9	21.0	10.8	62.9	6.9	33.1
Ramellogammarus spp.	2.8	16.2	1.2	36.8	0.8	40.0	1.1	32.4
Corophium spp.	85.3	97.3	95.1	98.7	87.8	97.1	90.9	98.0
Cladocera	0.4	5.4	0.3	14.5	<0.1	5.7	0.2	10.1
Cyclopoida	4.6	8.1			<0.1	2.9	0.3	2.7
Ceratopogonidae larvae			<0.1	1.3			<0.1	0.7
Diptera larvae and pupae	3.0	24.3	0.4	13.2	0.2	22.9	0.5	18.2
Ephemeroptera					<0.1	2.9	<0.1	0.7
Insecta					<0.1	2.9	<0.1	0.7
Empty stomachs	2.6		0.0		0.0		0.7	
With yolk sac	0.0		0.0		0.0		0.0	

*Frequency of occurrence

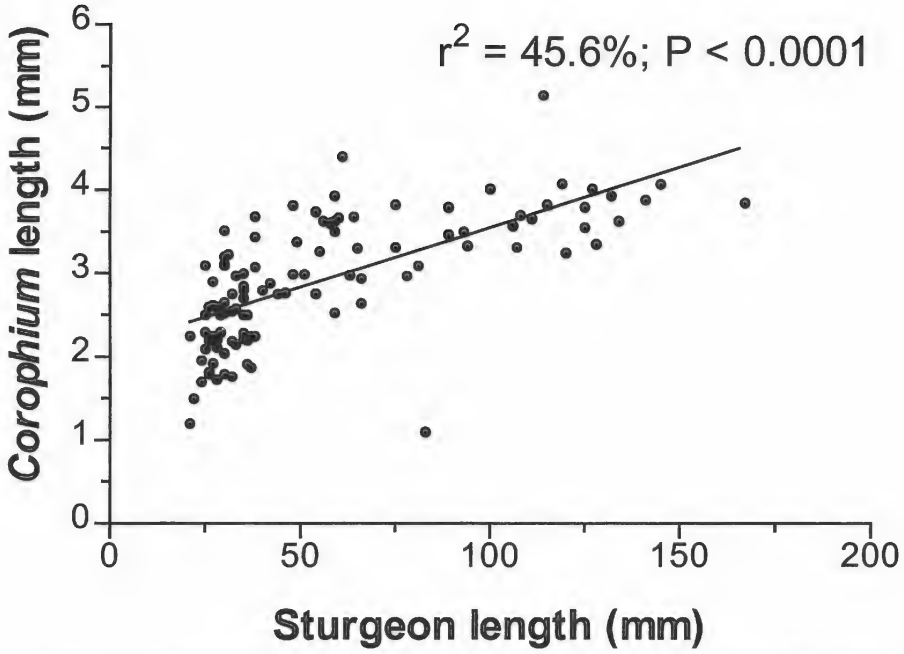

Figure 2. The relationship between the length (mm) of *Corophium* spp. found in larval and young-of-the-year white sturgeon stomachs and white sturgeon total length (mm) downstream from Bonneville Dam, 1990 and 1991.

had the highest percent number and percent frequency of occurrence in larvae and YOY white sturgeon stomachs each month in fish sampled downstream from Bonneville Dam and in the reservoirs (Tables 2 and 3). Downstream from Bonneville Dam, the proportion of the diet composed of *Corophium* spp. increased each month, and *Corophium* spp. were found in 100% of the stomachs from August through September/October (Table 2). In the reservoirs, *Corophium* spp. were found in > 97% of the fish examined in all months (Table 3). The length of *Corophium* spp. eaten downstream from Bonneville Dam increased significantly with increasing fish length ($r^2 = 45.6\%$, $P < 0.0001$)(Figure 2). The *Corophium* spp. eaten by white sturgeon were primarily *C. salmonis*, although *C. spinicorne* were also consumed.

Mean stomach fullness values ranged from 4.1 (26-50% full) in June to 5.1 (50-75% full) in August downstream from Bonneville Dam, averaging 4.5 in this reach (Table 1). In the reservoirs, mean stomach fullness ranged from 5.3 to 5.4, averaging 5.4.

Discussion

Corophium spp. were the dominant prey consumed by larval and YOY white sturgeon captured from both impounded and free-flowing sections of the Columbia River during this study, and were important in the diet of first-feeding fish. Mortality of larval fish is often greatest during the period of transition from endogenous to exogenous feeding (Hjort 1926). It is unknown when "irreversible starvation" or the "point-of-no-return" (May 1974) occurs for larval white sturgeon that are deprived of food. Exogenous feeding generally begins 8 to 14 days post-hatch, depending on water temperatures (Conte et al. 1988). Post-yolk-sac larval white sturgeon metamorphose into juveniles with a full compliment of fin rays and scutes after about 25 to 30 days (authors, unpublished data). During this time, fish actively feed on the substrate, but they do not have complete swimming capabilities. Priegel (1970) found that larval walleye (*Stizostedion vitreum vitreum*) were dependent on sufficient currents to carry them downriver to areas with suitable food within three

to five days of hatch. If river velocities were not sufficient, their yolks were depleted prior to entering habitat suitable for their primary prey, and they starved. Presumably, larval white sturgeon would fare similarly if appropriate food is not available at the onset of exogenous feeding.

Corophium spp. were also the most important prey for juvenile and sub-adult white sturgeon collected downstream from Bonneville Dam in the Columbia River (Muir et al. 1988, McCabe et al. 1993) and for YOY white sturgeon collected in the San Joaquin River, California (Schreiber 1962). The diets of YOY for other sturgeon species vary from primarily prey of benthic origin to planktonic origin (Kasumyan and Kazhlayev 1993, Ross and Bennett 1997). Post-larval lake sturgeon (*Acipenser fulvescens*) fed primarily on cladocerans and dipteran larvae in a Wisconsin lake (Kempinger 1996). Cladocerans and dipteran larvae were also eaten by white sturgeon larvae in our study, but were not the predominant prey. Food habit studies of larger white sturgeon have found that the dietary importance of fish and larger invertebrates increases with increasing fish size (Semakula 1963, Radtke 1966, Semakula and Larkin 1968, McKechnie and Fenner 1971).

The availability of *Corophium* spp. could play a key role in the survival of larval and YOY white sturgeon in the Columbia River and could possibly explain the apparent poor survival of larvae and YOY in some Snake and Columbia River reservoirs that apparently have successful spawning but poor recruitment (Parsley and Beckman 1994). Downstream from Bonneville Dam, YOY white sturgeon were captured primarily between RKm 45 and 166, with few collected in the 68 km of river immediately downstream from Bonneville Dam at RKm 234 (McCabe and Tracy 1994). They were found primarily on sand substrates, which are the predominant substrates in the lower Columbia River downstream from Bonneville Dam and in Bonneville Reservoir (Parsley and Beckman 1994). Sturgeon prefer sandy bottoms, where they can feed efficiently using their ventral barbels and protrusible mouths to suck prey from the substrate; they avoid vegetation, uneven substrates, and silt (Levin 1988, Sbikin and Bibikov 1988).

White sturgeon spawning in the Columbia River system occurs during high flows that disperse eggs and larvae downstream. Brannon et al. (1985) reported that white sturgeon larvae held in aquaria swam up in the water column for about a five-day period after hatching, then settled to the bottom where they stayed if food was present. If food was not found, larvae again swam to the surface. This behavior would increase their downstream displacement and is thought to be a mechanism for dispersal to suitable habitats. Nilo et al. (1997) suggested that lake sturgeon year-class strength in the Saint Lawrence River was determined in the first few months of life, and that climatic and hydrological conditions in June, while larvae were dispersing from spawning grounds and exogenous feeding began, were the critical elements. Stevens and Miller (1970) found a direct relationship between river flow and white and green sturgeon (*A. medirostris*) larval abundance in the Sacramento-San Joaquin Delta, California although river flow may have influenced their sampling efficiency to some degree.

The larval and smallest YOY white sturgeon examined in this study selected the smallest *Corophium* spp. This would be expected since sturgeon larvae are gape-limited and unable to handle larger prey. The spring and early summer timing of white sturgeon larvae coincides with the presence of juvenile *Corophium* spp. in the size range useable by larvae. Although little is known about *Corophium* spp. populations in the Columbia River, especially in reservoirs, most populations studied have produced offspring twice yearly in spring and fall (Higley et al. 1984). The distribution and density of *Corophium* spp. populations are related to sediment size, and their abundance would most likely vary throughout the reservoirs and downstream from Bonneville Dam (Higley et al. 1984, McCabe et al. 1997). Reservoirs typically change from coarse sediment or cobble in their upper reaches to fine sand or silt downstream (Vannote et al. 1980). Therefore, the degree to which white sturgeon larvae successfully disperse to suitable habitats could be dependent on the magnitude of spring flows, the effect of channel morphometry on velocities within each reservoir, and the length and sediment characteristics of each reservoir.

As post-larval size (especially mouth gape) and swimming performance increase, the range of suitable food sizes and types increases (Blaxter 1969). Rapid growth from the larval stage increases swimming performance and decreases predation risk and size-related vulnerability to predators in bloater (*Coregonus hoyi*) (Rice et al. 1997).

Swimming speed (sustained and burst) increases with larval length, giving larger larvae an advantage to capture food or avoid predation (Miller et al. 1988). Survival of striped bass larvae (*Morone saxatilis*) was related to prey availability, with greatest mortality occurring when endogenous energy sources (yolk and oil) were exhausted (Eldridge et al. 1981). Species having larger larvae, such as white sturgeon, may have a longer window to find prey, due to their relatively large size and available energy reserves. This could increase survival in environments where prey availability is patchy (Miller et al. 1988).

Sturgeon have high fecundity, with white sturgeon in the lower Columbia River found to produce from 98,200 to 699,000 eggs per female (DeVore et al. 1995), with potentially even more eggs produced by the largest spawners with estimates as high as 4.7 million eggs per female (Moyle 1976). Therefore, substantial mortality during the egg and larval stages is expected. Miller and Beckman (1996) observed white sturgeon eggs in the stomachs of four common fish species collected downstream from The Dalles, John Day, and McNary Dams in the Columbia River. Although no larvae or YOY were found in these predator stomachs during their study, their sampling occurred immediately downstream from spawning areas from which most larvae would have already been displaced. Some predation farther downstream during this life stage would be likely. Anders (1996) reported that a substantial number of naturally produced white sturgeon eggs collected from the Kootenai River, Idaho during 1994 and 1995, were recorded from stomach contents of native predatory fishes. Anders and Richards (1996) reported finding one white sturgeon larvae in the stomach of a northern pikeminnow, *Ptychocheilus oregonensis*.

In this study, larval and YOY white sturgeon diets from adjacent impounded and free-flowing sections of the Columbia River were similar and no evidence of larval starvation was found. The fish were sampled from areas that currently support healthy populations of white sturgeon. Thus, larval starvation may not be a determinant of year-class strength in these areas. Capturing starving or dead larval white sturgeon in reservoirs lacking robust populations would be difficult because they would most likely already be scavenged or preyed upon. In reservoirs that contain adult white sturgeon, but lack YOY and juveniles, determining if suitable food resources exist for survival of post-yolk-sac larvae would be a logical research direction. In reservoirs found lacking suitable food resources to support early sturgeon life stages, management options to enhance white sturgeon populations should be considered, including the release of older juvenile hatchery fish or supplementation with older juveniles collected elsewhere. Older white sturgeon would be able to utilize a wider variety of food items. Releases would need to be made in suitable locations within each reservoir and at a size sufficient to utilize available food resources.

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A Redwood Tree Whose Crown is a Forest Canopy

Abstract

Ancient redwood trees (*Sequoia sempervirens*) often have complex crowns consisting of multiple, resprouted trunks. This study focuses on a single redwood tree, which is known as the Redwood Creek Giant, growing in Tall Trees Grove of Redwood National Park, CA. It is the sixteenth tallest (109.8 m) known living tree and the twentieth largest (744.7 m^3 wood volume) known living redwood. The main trunk, which is 5.6 m in diameter at the base and still over 3 m in diameter at 65 m, is devoid of branches for 54 m. Above this height, its crown becomes a forest; there are a total of 148 resprouted trunks arising from the main trunk, other trunks, or branches. Five of these trunks exceed 1 m basal diameter, and twelve of them are between 0.5 and 1 m basal diameter. The largest resprouted trunk is 40 m long. Many of the trunks are fused to other trunks and/or branches. The tree's crown, which begins above 50 m, is over 25 m diameter 100 m above the ground. A variety of vascular plant species grow as epiphytes in this tree, including two ferns (*Polypodium scouleri* and *P. glycyrrhiza*), a shrub (*Vaccinium ovatum*), and two trees (*Lithocarpus densiflorus* and *Umbellularia californica*). The highest recorded epiphytic tree, an *U. californica*, grows from a knothole 98.3 m above the ground.

Introduction

The tallest and most massive forests on Earth are dominated by *Sequoia sempervirens* (D. Don) Endl. (hereafter 'redwood'). Individual redwood trees can reach 112 m in height, and individual redwood forest stands can have a biomass of over 3,000 metric tons per ha (Sawyer et al. 1999). Despite their impressive stature, however, very little was known about the biology of redwood forest canopies until the late 1990s, when rope-based canopy research began at Humboldt State University.

Like many other conifers, young redwood trees grow via a simple architectural model (sensu Hallé et al. 1978) consisting of a single vertically oriented trunk that supports numerous horizontally oriented branches. Older redwood trees, however, may have multiple resprouted trunks arising from other trunks and branches. These extra trunks are reiterations of the tree's architectural model, and each one supports its own system of branches. They appear to arise in response to increased light availability caused by either crown damage or the creation of nearby canopy gaps (Hallé et al. 1978, Sillett 1999). Reiterations in ancient redwood trees may account for over 10% of a tree's total wood volume (Sillett 1999).

Crown-level complexity promotes biological diversity in redwood forest canopies. A variety of vascular plants, including ferns, shrubs, and trees normally found on the forest floor, flourish in deep humus accumulations in ancient redwood tree crowns (Sillett 1999). The crown humus is also home to a variety of animals, including arthropods, mollusks, earthworms, and salamanders that breed in the canopy (pers. obs., Welsh and Wilson 1995). Rotten wood in dead branches and hollow trunks also provides substrates for ericaceous shrubs, which are pollinated by bees and produce abundant crops of berries that are consumed and dispersed by birds (Sillett 1999).

In the course of our investigations of old-growth redwood forest canopies, we encountered a redwood with an astonishing crown. From a distance, its broad crown could easily be mistaken for several large trees standing close together. Using rope-based methods of access, we explored this tree in order to quantify its crown structure and to assess the distribution and abundance of resident vascular epiphytes.

Study Area

This study focused on a single 109.8-m tall redwood in Redwood National Park, Humboldt County, California. The tree is known as the Redwood Creek Giant (hereafter 'RCG'). It grows at 37 m elevation in Tall Trees Grove, which is on an alluvial terrace of Redwood Creek. The old-

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growth forest canopy of the grove is overwhelmingly dominated by redwood. *Acer macrophyllum* Pursh, *Lithocarpus densiflorus* (Hook. & Arn.) Rehder, and *Umbellularia californica* (Hook. & Arn.) Nutt. occur in the understory and lower canopy. A few *Pseudotsuga menziesii* (Mirb.) Franco occur in the old-growth forest on the slope just east of the terrace. The forest across Redwood Creek was logged prior to Park acquisition in 1978. The RCG grows in a well-protected location at the northeastern edge of the terrace. Eighteen redwood trees over 90 m tall grow within a 100 m radius of it.

Methods

Tree Access

We accessed the RCG by shooting a rubber-tipped fiberglass arrow trailing 10 kg test strength Fireline® filament through a crotch formed by several reiterated trunks at 70 m with a compound bow mounted to a spinning reel. A 3 mm nylon cord, followed by an 11 mm static kernmantle climbing rope, was then hauled over the crotch. We anchored one end of the rope at ground level and climbed the other using mechanical ascenders. We used a 20 m long arborist's rope lanyard fitted with a double-end, split-tail system (Sherrill Arborist Supply, Inc.) to access progressively higher trunks and branches and to move laterally through the crown. A rescue pulley was secured near the top of the tree with a tubular nylon webbing sling. The climbing rope was lowered from the tree on nylon cord at the end of the day, and the pulley was used to haul the rope back into place for subsequent ascents. We explored the tree crown for seven days in December 1998 and January 1999.

Crown Mapping

We mapped crown structure of the RCG by measuring heights, diameters, and distances between reiterated trunks. The tree's total height was measured by lowering a graduated fiberglass tape from the topmost foliage to the forest floor with ground contact via radio. Numbered aluminum tags were attached to major trunks at 5 m intervals with 2 cm paneling nails. We used these tags as benchmarks for height measurements of smaller trunks, branches, and epiphytes. Aluminum tags were also used to label individual trunks for future reference. We recorded the following data for each reiterated trunk: top height, height of origin, basal diameter, and diameter at 5 m intervals along the length of the trunk. For reiterated trunks arising from branches, we also recorded horizontal distance to main trunk, branch height, branch basal diameter, and branch diameter at reiteration. Trunks were referenced to each other by recording azimuths and distances between them at 5 m height intervals. We used an Impulse® laser range finder (Laser Technology, Inc.) to measure vertical and horizontal distances between trunks. All other measurements were made with the aid of a compass, clinometer, and graduated fiberglass tape. Since large trunks often gave rise to complex arrays of smaller trunks, we sketched crown structure and noted physical connections between trunks and branches. We also noted whether trunks were monopodial (i.e., consisting of a single axis), sympodial (i.e., consisting of successive axes), or otherwise broken. All of this information was used to generate a tree crown diagram via DeltaGraph® and ClarisDraw® software for the Macintosh® computer.

Crown Illustration

In addition to mapping crown structure, we also made a detailed illustration of the entire tree as visible from Redwood Creek. Major branches, clumps of foliage, burls, and kinks were noted on a sketch, and heights to these landmarks were measured with the Impulse® laser. We then took photographs of all portions of the crown from as far away from the tree as possible. The illustration itself started with a 'skeleton,' which was based on the height and diameter measurements taken both from within the crown and from the ground. We used the photographs to provide details of foliage, branches, and bark texture. The illustration was drawn at 1/120 scale, and people were added for additional scale.

Epiphyte Sampling

We nondestructively measured sizes and locations of all vascular epiphytes occurring on the RCG. For each fern mat, we measured number of living fronds, maximum frond length, maximum frond order (i.e., rows of pinnae per frond), mat length, and mat width. For each shrub, we measured number of stems, maximum stem basal diameter, total length, and maximum crown width.

Similarly, we measured trunk basal diameter, total length, and maximum crown width for epiphytic trees. In addition to these variables describing epiphyte size, we measured height above ground, distance and azimuth to main trunk, and diameter of supporting branch beneath epiphyte (if present).

Data Analyses

We used linear regression analysis to explore relationships between crown structure variables (i.e., height of origin, total length, basal diameter, wood volume, distance from main trunk, branch basal diameter, and branch diameter at reiteration). Correlations were separately evaluated for all reiterated trunks and for the subset of reiterated trunks arising from branches. Wood volume was calculated by applying two different equations to the trunk diameter data. We used the equation for a parabolic frustum (i.e., volume = length/2*[A1 + A2], where A1 and A2 are the upper and lower trunk cross sectional areas) for reiterated trunks and upper sections of the main trunk that tapered rapidly. We used the equation for a regular conic frustum (i.e., volume = length*π/3*[lower diameter^2 + (lower diameter)*(upper diameter) + upper diameter^2]) for sections of the main trunk that tapered slowly.

Results

Crown Structure

At 109.8 m (360.2 feet) tall and 744.7 m^3 (26,298 feet^3) wood volume, the RCG is the sixteenth tallest known living tree and the twentieth largest known living redwood (Figure 1, Sawyer et al. 1999). The most remarkable feature of the RCG, however, is neither its height nor its wood volume. There are a total of 148 reiterated trunks arising from the main trunk (n = 12), other trunks (n = 81), or branches (n = 55). Five of these trunks exceed 1 m basal diameter, and twelve of them are between 0.5 and 1 m basal diameter (Figure 2). The RCG's reiterations account for 14 percent of its total wood volume.

Trunk wood volumes in the RCG span seven orders of magnitude (Figure 3). Reiterated trunks arising from the main trunk are up to ten times larger than the largest trunks arising from other reiterations (Figure 3). Thirty-three of the RCG's trunks give rise to other reiterations, and wood volume of the reiterations is positively correlated with the wood volume of the supporting trunk (Table 1). Trunk wood volume is also positively correlated with total length, basal diameter, and branch diameter at reiteration (Table 1).

In addition to those involving wood volume, there are several other significant correlations among the crown structure variables (Table 1). Longer trunks tend to occur lower in the crown; height of origin is negatively correlated with total length. Longer trunks also tend to occur on larger branches; branch diameter at reiteration is positively correlated with total length. Thicker branches support larger trunks than thinner branches; branch basal diameter and branch diameter at reiteration are positively correlated with trunk basal diameter. Finally, trunk basal diameter is strongly correlated with total length.

A more detailed description of the RCG proceeds with an examination of the crown illustration (Figure 4) and the crown diagram (Figure 5). Unlike most other tall (i.e., over 105 m) redwoods, whose upper crowns are usually thin and spindly, the RCG has a very top-heavy crown. The main trunk, which is 5.56 m diameter at the base and still over 3 m diameter at 65 m, is devoid of branches for 54 m. Above this height, its crown proliferates. Eleven trunks extend above 105 m, twenty trunks extend above 100 m, and the crown diameter between 70 and 100 m is over 25 m.

The first major reiteration (hereafter 'trunk I') emerges from the main trunk at 53.8 m (right side of Figure 5). A massive burl from the main trunk is fused with it between 57.2 and 59.4 m, and the diameters of both trunks are greater above the fusion than below it. Trunk I, which is 1.1 m basal diameter, 31.3 m long, and 14.8 m^3 wood volume, supports 42 other reiterated trunks. Most of these trunks arise from a complex array of branches up to 6 m long and 74 cm basal diameter. The three largest branches in this array are fused together in several places.

Four reiterations emerge from the main trunk between 66.1 and 69.9 m (left side of Figure 5). Their precise origins are difficult to determine because a deep layer of crown humus supporting ferns and shrubs has accumulated in the crotch (hereafter 'main crotch') formed at the base of these trunks and the main trunk. The largest of the reiterations (hereafter 'trunk II') forming the

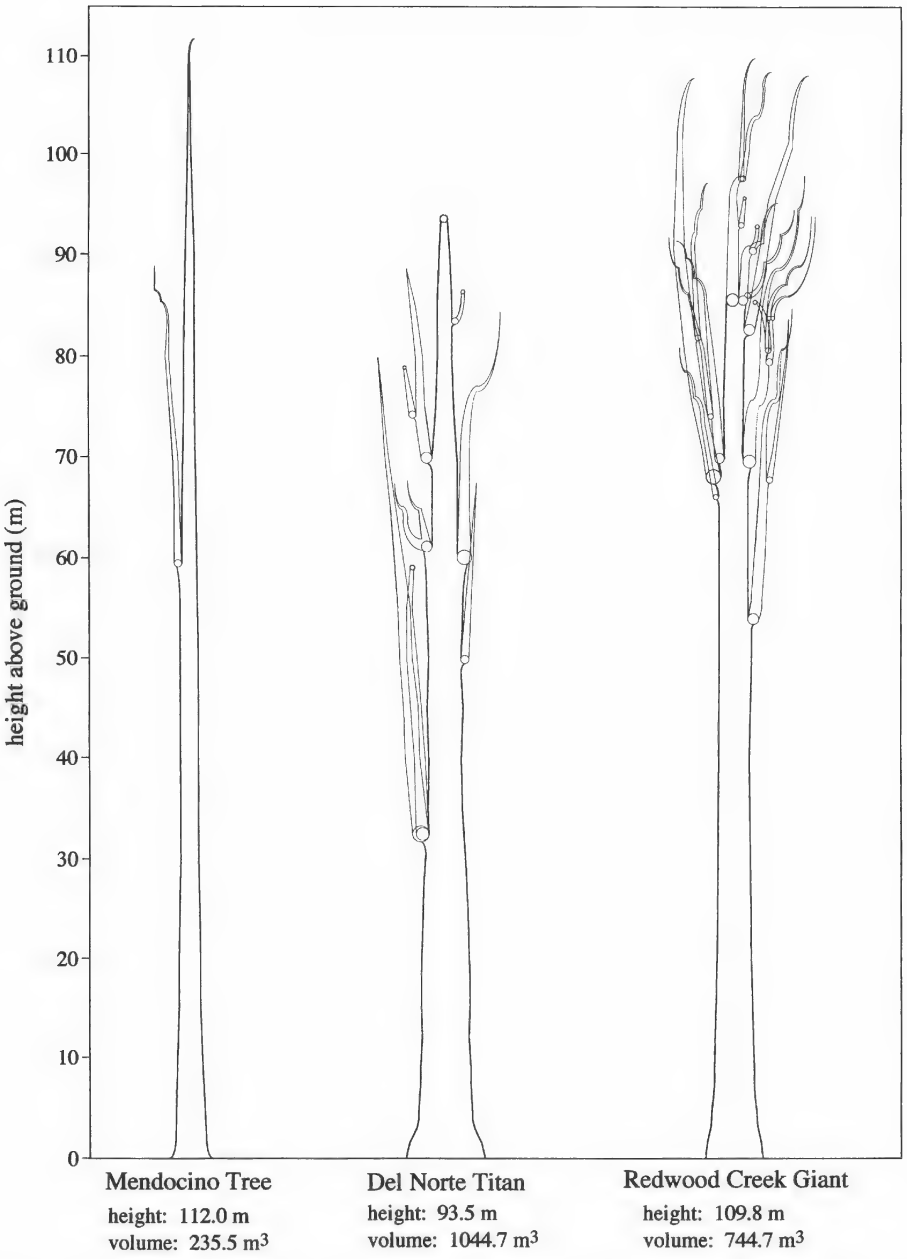

Figure 1. Scale diagram comparing crown structures of the tallest (Mendocino Tree, Montgomery Woods State Reserve, CA) and largest (Del Norte Titan, Jedediah Smith Redwoods State Park, CA) known living redwoods to the Redwood Creek Giant. Circles correspond to the basal diameters of reiterated trunks. Only trunks greater than 0.5 m basal diameter are shown. For each tree, distances between reiterated trunks are drawn relative to the presumed central axis of its main trunk. All distances are drawn to the scale of the y-axis.

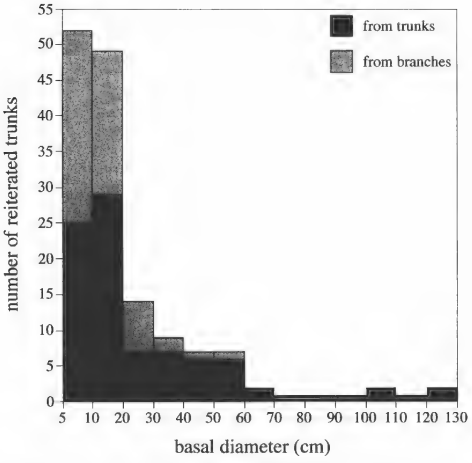

Figure 2. Size distribution of reiterated trunks on the Redwood Creek Giant by basal diameter. Trunks arising from other trunks are distinguished from those arising from branches.

main crotch is 1.3 m basal diameter, 40.0 m long, and 28.6 m^3 wood volume. Trunk II is the largest reiteration on the RCG, and it supports 21 other reiterated trunks. Above 90 m, most of these trunks sweep to the south, having been sculpted by winds moving up Redwood Creek from the Pacific Ocean. Several of trunk II's reiterations are fused together, including two trunks that are fused to the same branch. Many of the lesser reiterations on trunk II and the other trunks emerging from the main crotch are sympodial, having lost successive leaders in storms. Another reiteration (hereafter 'trunk III') emerging from the main crotch is 1.0 m basal diameter, 20.7 m long, and 6.5 m^3 wood volume. Trunk III and most of its 14 reiterated trunks extend out into the large canopy gap above the Tall Trees Grove loop trail.

Another major reiteration (hereafter 'trunk IV') emerges from the main trunk at 69.6 m (right side of Figure 5). Trunk IV is 1.3 m basal diameter, 28.8 m long, and 13.6 m^3 wood volume. It supports

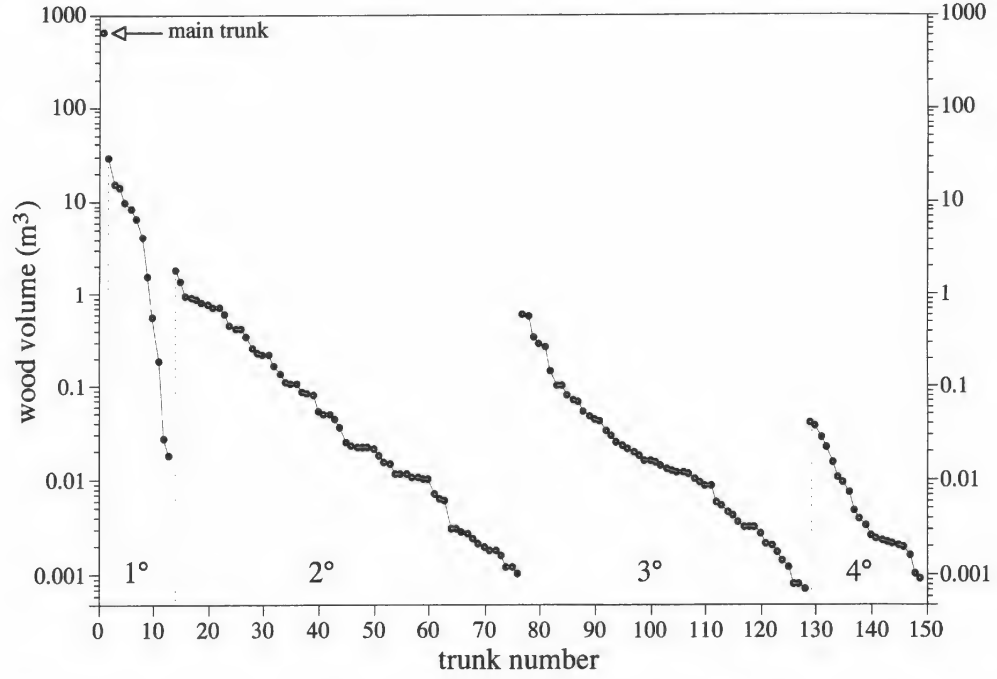

Figure 3. Ranked size distribution of trunks on the Redwood Creek Giant by reiteration hierarchy and wood volume. Trunks are separated into five classes (i.e., main, 1°, 2°, 3°, and 4°) on the basis of reiteration hierarchy. Reiterations arising directly from the main trunk are considered primary (1°) trunks, reiterations arising directly from 1° trunks are considered secondary (2°) trunks, and so on.

TABLE 1. Summary of product-moment correlation coefficients (r) between crown structure variables for reiterated trunks on the Redwood Creek Giant. Broken trunks (n = 13) were excluded from correlations for total length and volume. Correlations for supported wood volume were based only on unbroken trunks that supported other reiterated trunks (n = 25). Correlations statistically significant ($P \leq 0.01$) are highlighted in bold.

All reiterated trunks (n = 148)

	Height of origin	Total length	Basal diameter	Wood volume
Total length	**-0.31**			
Basal diameter	-0.14	**0.92**		
Wood volume	-0.20	**0.84**	**0.81**	
Supported wood volume	**-0.46**	**0.82**	**0.87**	**0.86**

Reiterated trunks arising from branches (n = 55)

	Height of origin	Total length	Basal diameter	Wood volume	Distance from main trunk	Branch basal diameter
Total length	-0.29					
Basal diameter	-0.20	**0.89**				
Wood volume	0.00	**0.73**	**0.88**			
Distance from main trunk	-0.28	-0.14	-0.28	-0.27		
Branch basal diameter	-0.32	0.29	**0.41**	0.31	-0.08	
Branch diameter at reiteration	-0.27	**0.50**	**0.68**	**0.47**	-0.28	**0.67**

27 other reiterated trunks, including three trunks with snapped tops. Trunk IV itself is sympodial with a complex history of breakage and reiteration. A dead, snapped trunk leads into a rotten hollow near its base. A 0.7 m diameter trunk arises from trunk IV at 79.5 m. It is forked at 83.9 m, and both lesser trunks reach almost 95 m. A branch from one of these lesser trunks is completely fused with the other trunk at 85.0 m (not shown in Figure 5). Remarkably, this 11.1 m long branch remains alive and vigorous despite the fact that it is now detached from its trunk of origin. An 8 cm gap now separates the branch from its original source of water and nutrients. Since breaking away, the diameter of this transplanted branch has increased by 2 cm.

At 82.7 m, yet another major reiteration (hereafter 'trunk V') emerges from the main trunk (right side of Figure 5). Trunk V is 1.1 m basal diameter, 25.9 m long, and 9.5 m^3 wood volume. It supports five other reiterated trunks.

The main trunk is snapped at 85.4 m, where it gives rise to 3 major reiterations. The largest of these (hereafter 'trunk VI') is 1.1 m basal diameter, 12.3 m long, and 8.0 m^3 wood volume. It supports 12 other reiterated trunks. At 97.7 m, trunk VI is broken and gives rise to two reiterations, including the trunk bearing the highest foliage on the RCG. Two of trunk VI's reiterations are broken with snapped tops. Trunk VI is fused with another major reiteration (hereafter 'trunk VII') at 88.1 m. Trunk VII is 0.9 m diameter at the base, 1.0 m diameter above the fusion, and 8.2 m long with a broken top. It gives rise to 11 other reiterated trunks, including one broken and one sympodial trunk. An old raven (*Corvus corax*) nest is perched in the crotch formed by trunk VII and the other trunk (hereafter 'trunk VIII') arising from the snapped top of the main trunk. Just above the nest, a branch from trunk VII is fused with trunk V, although the branch is now dead. Trunk VIII is sympodial and extends out into a crown gap near the top of trunk IV.

Epiphyte Distribution

We found five species of vascular epiphytes growing on the RCG (Table 2). The shrub *Vaccinium ovatum* is the most numerous species with 10 individuals. Eight of the shrubs grow on dead branches, from the tops of broken trunks, or from rotten hollows in trunks that lacked crown humus accumulations. Two of the shrubs grow from

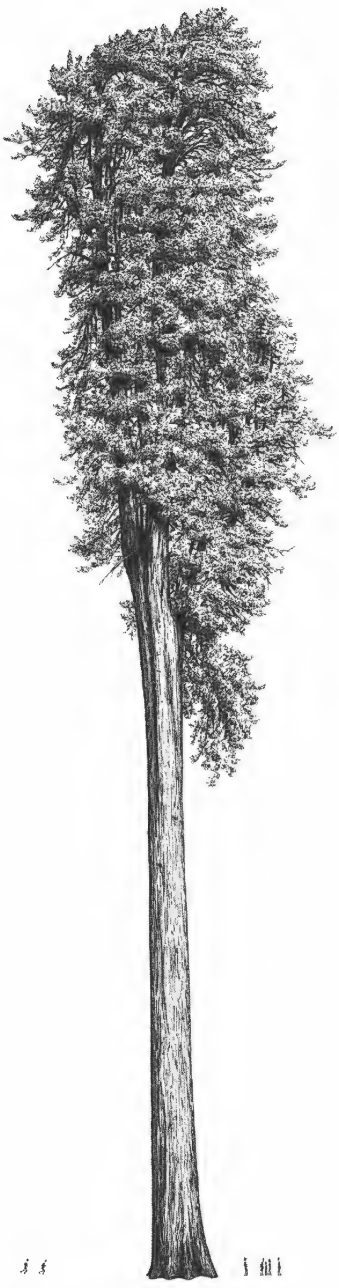

Figure 4. Illustration of the Redwood Creek Giant prepared by Dr. Robert Van Pelt on the basis of crown structure data and photographs taken from Redwood Creek.

deep (i.e., > 50 cm) humus in the main crotch. This crown humus is also exploited by ferns, including one of the largest epiphytes on the tree: a *Polypodium scouleri* fern mat with 36 fronds up to 75 cm long. A small *P. glycyrrhiza* fern mat also grows in the main crotch. Crown humus and epiphytes in the main crotch store water, some of which drips down the trunk to form a splash zone that is exploited by a lush growth of bryophytes. Two fern mats, one of each species, grow beneath the raven nest in the crotch formed by trunks VII and VIII. One *P. glycyrrhiza* mat grows on the top of a broken trunk at 92.1 m. Two *P. glycyrrhiza* mats grow on dead branches at 86.7 m and 83.2 m. Three epiphytic trees grow on the RCG. One *Umbellularia californica* grows on a dead branch at 84.8 m. Another *U. californica* grows from trunk II at 98.3 m. It may be the highest vascular epiphyte on Earth. Finally, a *Lithocarpus densiflorus* grows on a dead branch at 82.1 m.

Discussion

The RCG is neither the tallest nor the largest living redwood, but it certainly has one of the most complex crowns. No known redwood has as many reiterations as the RCG; the most complex redwood previously studied has only 62 reiterated trunks (Sillett 1999). The cause of the RCG's tremendous crown-level complexity is unknown, but repeated exposures to crown fires and high winds probably contributed to it. Evidence of crown fires is commonly observed in ancient redwood trees (Sillett 1999). Several fire scars are evident beneath the break in the RCG's main trunk at 85.4 m, suggesting that its original trunk may have been lost during a fire. The RCG's upper crown is exposed to high winds during storms, and wind-sculpting of the trunks and branches is evident, especially above 90 m. While exploring the upper crown in early December, we were suddenly hit by a storm with gale-force winds. The major reiterations swayed back and forth wildly. Such independent movement of reiterated trunks initiates wound responses as sections of the crown abrade one another in the wind. Ultimately, many such wounds lead to fusions between trunks and branches.

The prevalence of trunk-to-trunk (n = 7), trunk-to-branch (n = 11), and branch-to-branch (n = 3) fusions in the RCG indicate that the hydraulic architecture of its crown is convoluted. Fusions

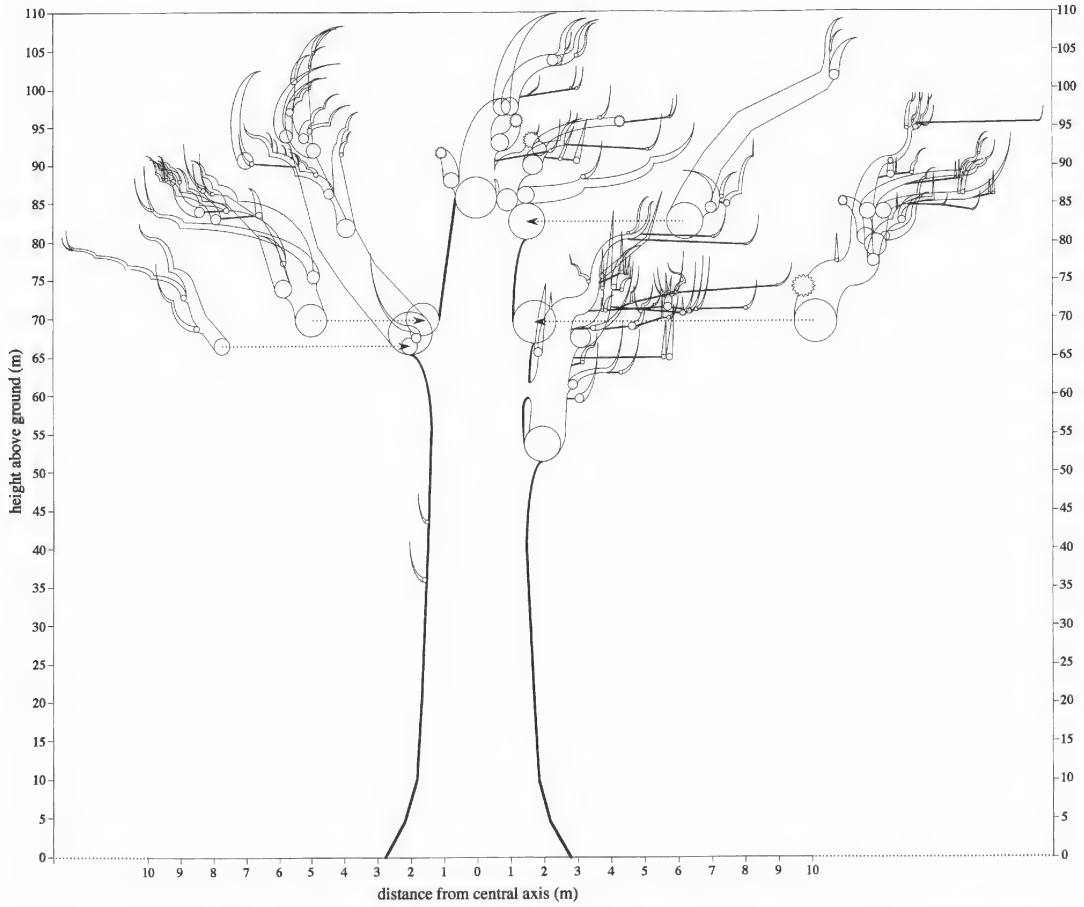

Figure 5. Crown diagram of the Redwood Creek Giant. Unlike Figure 1, all trunk diameters are drawn to the scale of the x-axis, which is expanded relative to the scale of the y-axis. Circles correspond to the basal diameters of reiterated trunks. Circles with serrated edges indicate broken trunks. Branches bearing reiterated trunks are depicted with single straight lines. No other branches are shown.

TABLE 2. Summary of vascular plants occurring as epiphytes in the crown of the Redwood Creek Giant. Mean values for each variable are listed along with ranges in parentheses.

Species	N	Height above ground (m)	Size of tree, mat, or shrub		Number of stems or fronds	Maximum stem diameter (mm)	Maximum frond length (cm)
			length (cm)	width (cm)			
Lithocarpus densiflorus	1	82.2	31.0	15.0	1.0	3.0	—
Polypodium glycyrrhiza	5	82.7 (66.5–92.1)	37.4 (15.0–80.0)	17.8 (1.0–45.0)	13.6 (3.0–23.0)	–	19.2 (9–27)
Polypodium scouleri	4	77.3 (66.7–89.8)	65.5 (20.0–180.0)	30.2 (5.0–70.0)	14.2 (3.0–36.0)	– (6–75)	35.0
Umbellularia californica	2	91.6 (84.8–98.3)	28.5 (22.0–35.0)	6.5 (5.0–8.0)	1	5.5 (3.0–8.0)	–
Vaccinium ovatum	10	84.0 (66.2–95.3)	80.2 (16.0–176.0)	89.4 (31.0–225.0)	8.5 (2.0–38.0)	12.6 (3.0–22.0)	–

divert the flow of water and nutrients through the tree's vascular tissues. Two pieces of evidence support this assertion. First, trunk diameters are consistently greater above fusions than below them (see also Sillett 1999). Second, the branch on trunk IV that fused with another trunk survives even though it is no longer attached to its original trunk. In addition to affecting the RCG's hydraulic architecture, crown fusions may increase the tree's architectural strength, thus reducing the severity of crown breakage during storms. They also provide platforms for humus accumulation and epiphytes.

The deepest crown humus accumulation, which occurs in the main crotch, supports the richest growth of vascular epiphytes on the RCG. Compared to many other large redwood trees, however, the RCG is rather depauperate in crown humus and vascular epiphytes. Most of the RCG's epiphytes occur close to the central axis of the tree either in crotches or on rotten wood above the break in the main trunk. Very few vascular epiphytes inhabit the massive reiterated complexes sprouting from the main trunk below 85 m; crown humus accumulations are completely lacking.

Crown humus and vascular epiphytes are often abundant far from the main trunk on reiterations in large redwoods of Prairie Creek Redwoods State Park and Jedediah Smith Redwoods State Park (Sillett 1999). Occurrence of the RCG in a drier microclimate than these areas may account for this difference. Tall Trees Grove lies in the rain shadow of a steep 400-800 m tall ridge that protects Redwood Creek from the ocean, while the groves studied by Sillett (1999) are more exposed to moisture-laden air coming directly from the ocean. Rarity of vascular epiphytes in the tall redwood forests of Humboldt Redwoods State Park and Montgomery Woods State Reserve (pers. obs.), both of which are located inland away from direct ocean influence, supports this hypothesis. Thus, despite its unrivaled complexity, most of the RCG's crown may be inhospitable to vascular epiphytes requiring year-round access to a moist substrate.

Only one species of vascular epiphyte growing on the RCG has not been previously observed on other redwoods. *Umbellularia californica* is a common understory tree in many redwood forests. Its fleshy drupes must have been dispersed high into the crown of the RCG by birds. The individual growing at 98.3 m had only four living leaves, and its roots were located 20 cm down inside a knothole that collects stemflow.

In conclusion, the RCG challenges our concepts of individual tree crowns and forest canopies. In normal usage, trees have crowns and forests have canopies. With 148 reiterated trunks, several of which are as large as full-size trees in other forests, the crown of the RCG can be viewed as a forest canopy. This tree and others like it dramatically illustrate that the distinction between trees and forests is a small one.

Acknowledgements

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Vertical Distribution of Dominant Epiphytes in Douglas-Fir Forests of the Central Oregon Cascades

Abstract

The canopies of old-growth Douglas-fir forests support a diversity of epiphytic lichens and bryophytes. We quantified the vertical distributions of six dominant epiphytes throughout the crowns of large *Tsuga heterophylla* (46–57 m tall) and *Pseudotsuga menziesii* (60–78 m tall) trees in five forest stands of the central Oregon Cascades. There were no major differences in epiphyte distribution between the two tree species, but epiphytes on *T. heterophylla* generally peaked in abundance at heights 10–20 m below those on *P. menziesii*. Alectorioid lichens were most abundant in the upper crowns but scarce in the lower crowns. The fruticose green algal lichen *Sphaerophorus globosus* was evenly distributed throughout the crowns. The cyanolichen *Lobaria oregana* and the moss *Antitrichia curtipendula* were most abundant in middle crowns. *Lobaria pulmonaria* was most abundant in the lower–middle crowns. It was scarce or absent in the upper crowns. The moss *Isothecium myosuroides* was also scarce or absent in the upper crowns. It was most abundant in the lower crowns. The vertical patterns described in this study are not representative of all old-growth Douglas-fir forests. In wetter forests, bryophytes are dominant throughout the canopy. In drier forests, alectorioid and other green algal lichens extend farther down in the canopy, and bryophytes and cyanolichens are restricted to the lower canopy.

Epiphytes are a conspicuous and ecologically significant component of forests in the Pacific Northwest, where they have been studied for over 25 years. A great deal is known about their floristics (Pike et al. 1975), community dynamics (Sillett 1995, Sillett and McCune 1998, Sillett et al. 2000a), population dynamics (Rhoades 1983), tree-level biomass (Pike et al. 1977, Sillett 1995), stand-level biomass (McCune 1993, Neitlich 1993), distribution by functional groups (Lyons 1998, McCune 1993, McCune et al. 1997, Sillett and Neitlich 1996), roles in nutrient cycling (Carroll 1979, Denison 1973, 1979, McCune and Daly 1994, Pike 1978), growth rates (Denison 1988, Rhoades 1977, Sillett 1994, Sillett and McCune 1998, Sillett et al. 2000b), dispersal limitations (Sillett et al. 2000b), vulnerability to edge effects (Sillett 1994, 1995), and susceptibility to forest management practices in old-growth Douglas-fir forests (Goward 1995, Peck and McCune 1997, Sillett and Goslin 1999, Sillett and Goward 1998, Sillett et al. 2000b). However, little quantitative information on vertical distributions of epiphytes on different tree species in these forests is currently available. The purpose of this study is to describe the vertical distributions of dominant epiphytes on two tree species, *Tsuga heterophylla* (Raf.) Sarg. and *Pseudotsuga menziesii* (Mirb.) Franco. We estimated the abundance of six epiphytes throughout the crowns of ten tall trees.

Study Area

We sampled epiphytes in five old-growth forest stands within the Willamette National Forest in the Cascade Range of western Oregon: three in the H. J. Andrews Experimental Forest, one along the South Santiam River near House Rock Forest Camp, and one along the South Fork McKenzie River near Cougar Reservoir (see Sillett et al. 2000b for more specific information). The stands were 450 to 600 years of age, 470 to 790 m elevation, 0 to 120° aspect, and 60 to 85 m tall. They were dominated by *Pseudotsuga menziesii* with smaller amounts of *Tsuga heterophylla*, *Thuja plicata* Donn., *Taxus brevifolia* Nutt., *Acer macrophyllum* Pursh., and *Alnus rubra* Bong. Basal areas ranged from 91 to 199 m^2ha^{-1} for conifers and 0.2 to 6.4 m^2ha^{-1} for hardwoods. Average annual precipitation in the stands ranged from 1.5 to 2.4 m (Oregon Climate Service). These stands have been utilized in previous epiphyte studies (Sillett et al. 2000ab).

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TABLE 1. Dimensions of ten study trees in the Willamette National Forest in western Oregon. The five forest stands are listed from north to south. All measurements are in meters.

Stand	*Tsuga heterophylla* tree height	*Tsuga heterophylla* tree dbh	*Pseudotsuga menziesii* tree height	*Pseudotsuga menziesii* tree dbh	notes
1	57.0	0.81	64.0	2.64	main trunk snapped at 61 m
2	52.0	0.97	60.5	1.86	main trunk snapped at 57 m
3	46.0	0.81	73.5	1.99	—
4	54.5	1.02	66.5	1.46	—
5	48.5	0.97	77.5	1.89	—

Methods

Tree Selection and Access

In each stand, we selected one large *P. menziesii* and the largest healthy *T. heterophylla* for detailed study. More specific information about each tree is summarized in Table 1. Tree crowns were accessed by shooting a monofilament over sturdy branches with a compound bow, hauling a nylon cord followed by a climbing rope over the branches, tying one end of the rope at ground level, and ascending the other end using vertical rope technique. We used 20-m long arborist's rope lanyards to access progressively higher branches and move laterally through tree crowns. Tree heights were measured by lowering a graduated fiberglass tape from the topmost foliage to the forest floor. Numbered aluminum tags were then attached to the main trunks at 10 m intervals. These tags were used as benchmarks for epiphyte sampling.

Epiphyte Sampling

We visually estimated epiphyte abundances within each 10 m stratum. Epiphyte abundance was recorded on a 0–6 scale: 0) absent, 1) 1–3 individual thalli, 2) up to 5% cover, 3) 5–10% cover, 4) 10–25% cover, 5) 25–50% cover, and 6) greater than 50% cover. We considered only six prominent branch-dwelling epiphytes that were easily recognized from the climbing path on each tree: 1) alectorioid lichens (i.e., mostly *Alectoria sarmentosa* with smaller amounts of *A. vancouverensis*, *Bryoria* spp., and *Usnea* spp.), 2) the green algal fruticose lichen *Sphaerophorus globosus*, 3) the cyanolichen *Lobaria oregana*, 4) the cyanolichen *Lobaria pulmonaria*, 5) the moss *Antitrichia curtipendula*, and 6) the moss *Isothecium myosuroides*. Finally, we visually estimated the average crown radius within each 10 m stratum to the nearest 0.5 m.

Results and Discussion

All of the epiphytes sampled in this study have similar distribution patterns on both tree species. The few discrepancies are attributable to differences in tree stature alone. Epiphytes on *T. heterophylla*, whose average height is 52 m, peak in abundance at heights 10–20 m below those on *P. menziesii*, whose average height is 68 m. Epiphytes are absent above 60 m on *T. heterophylla* simply because the tallest tree is only 57 m.

Vertical distributions of the six epiphytes differ greatly (Figure 1). Abundance of alectorioid lichens steadily increases from the lower to upper tree crowns. They cover over 25% of substrates above 50 m on *P. menziesii* and above 40 m on *T. heterophylla*. Old-growth Douglas-fir forests can support over 500 kg ha^{-1} of these lichens (Neitlich 1993, Sillett and Goslin 1999). *Sphaerophorus globosus* is more evenly distributed than any other epiphyte in this study, covering 5–10% of substrates throughout crowns of both tree species. This lichen is prevalent on trunks and branches in the inner crown, but it is scarce on branchlets and twigs in the outer crown (Lyons 1998, Sillett and Goslin 1999). *Lobaria oregana* is most abundant between 40 and 60 m on *P. menziesii* and between 30 and 50 m on *T. heterophylla*, where it covers over 25% of substrates. This is the dominant epiphyte in humid old-growth Douglas-fir forests with a biomass of 900–2600 kg ha^{-1}, which is 60–80% of the total lichen biomass (McCune 1994, Neitlich 1993, Pike 1978). A closely related species, *L. pulmonaria*

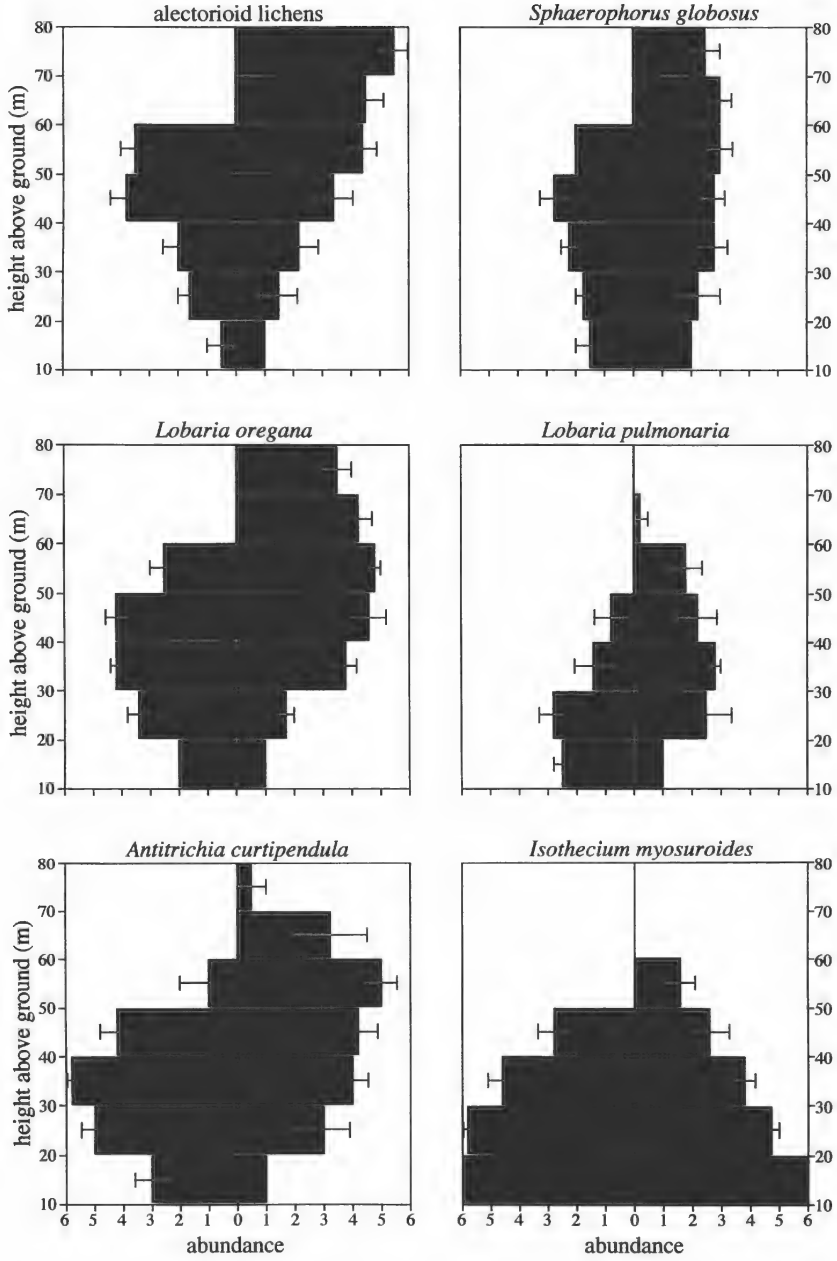

Figure 1. Vertical distribution of six epiphytes in humid old-growth Douglas-fir forests of the central Oregon Cascades. For each epiphyte, the distribution on *Tsuga heterophylla* is shown on the left, and the distribution on *Pseudotsuga menziesii* is shown on the right. Abundance is on a 6–point, logarithmic scale (see Methods). Values are means and standard errors (n = 5 trees per tree species). Note that *T. heterophylla* trees were considerably shorter than *P. menziesii* trees (see Table 1 and Figure 2).

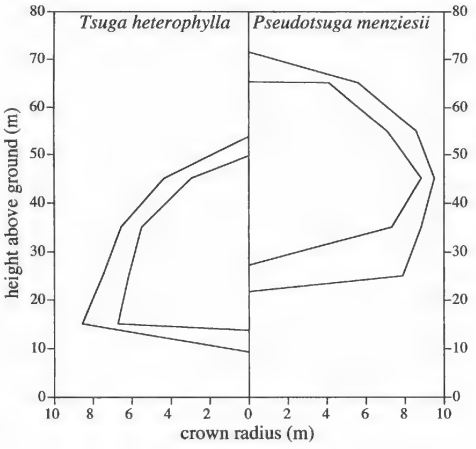

Figure 2. Crown profiles of *Tsuga heterophylla* and *Pseudotsuga menziesii* trees surveyed in this study. Inner and outer boundaries represent one standard error below and above the mean radii of the live crowns (n = 5 trees per tree species).

accounts for 3–19% of the total lichen biomass in such forests (McCune 1994, Neitlich 1993, Sillett 1995). It is most abundant between 30 and 40 m on *P. menziesii* and between 10 and 30 m on *T. heterophylla*, where it covers over 10% of substrates. Unlike *L. oregana*, which can tolerate exposed sites in the upper canopy (Sillett 1995), *L. pulmonaria* is virtually absent above 60 m on *P. menziesii* and above 50 m on *T. heterophylla*. The moss *Antitrichia curtipendula* is most abundant between 30 and 60 m on *P. menziesii* and between 20 and 50 m on *T. heterophylla*, where it covers over 25% of substrates. It forms extensive mats up to 10 cm thick on large branches, and individual trees can support up to 7 kg dry weight of this species (Sillett 1995). The moss *Isothecium myosuroides* is most abundant below 30 m, where it covers 25–50% of substrates on *P. menziesii* and over 50% of substrates on *T. heterophylla*. Unlike *A. curtipendula*, it is sparsely distributed in the upper canopy and absent above 60 m on *P. menziesii* and above 50 m on *T. heterophylla*. We did not record any epiphytes below 10 m because the study trees have no branches below this height (Figure 2). However, *I. myosuroides* is prevalent on the lower branches of smaller *T. heterophylla* trees as well as on understory vegetation (Lyons 1998, Pike et al. 1975).

The vertical distribution of an epiphyte species generally reflects its sensitivity to desiccation and ability to attain positive net photosynthesis at low water contents (Hosokawa et al. 1964, Tobiessen et al. 1977). In tall Douglas-fir trees, some species (e.g., alectorioid lichens and other green algal lichens) prefer exposed sites in the upper, outer crowns, while others (e.g., several cyanolichens and many bryophytes) prefer sheltered sites in the lower, inner crowns (Sillett 1995). Such preferences are probably the result of an interplay between desiccation tolerances and competitive abilities. For example, a desiccation-sensitive moss may not be able to survive in the xeric environment of the upper canopy, while a desiccation-tolerant lichen may not be able to compete with aggressive mat-forming mosses in the mesic environment of the lower canopy. Based on the vertical distributions documented in this study, the epiphytes may be tentatively ranked from highest to lowest desiccation tolerance or from lowest to highest competitive ability as follows: 1) alectorioid lichens, 2) *Sphaerophorus globosus*, 3) *Lobaria oregana*, 4) *Antitrichia curtipendula*, 5) *Lobaria pulmonaria*, and 6) *Isothecium myosuroides*. Ecophysiological and transplant experiments are needed to test this hypothesis.

The patterns documented in this study should not be considered representative of all old-growth Douglas-fir forests, because there is high landscape-level variability in epiphyte distribution depending on moisture regime (McCune 1993). An intermediate moisture regime favors a canopy epiphyte community with high cyanolichen diversity, whereas forests on the wetter or drier ends of the moisture gradient are more dominated by bryophytes or green algal lichens, respectively. In wet forests, bryophytes can dominate the entire vertical profile. For example, bryophytes are super-abundant in the rain forests of Olympic and Mount Rainier National Parks, Washington (pers. obs.), where mosses normally found on the forest floor also flourish as epiphytes (Sillett and Neitlich 1996). These rain forest canopies are so mossy that epiphytic lichens, including cyanolichens, are much less abundant than in the central Oregon Cascades (Sillett and Goward 1998). In dry forests, vertical ranges of alectorioid and other green algal lichens extend farther down in the canopy (Sillett 1995), while bryophytes and cyanolichens become restricted to the lower canopy

(Goward 1995). Such drier forests support a smaller biomass of bryophytes and cyanolichens, but alectorioid and green algal lichens are abundant (Howe 1978, Sillett unpubl.). Even the old-growth Douglas-fir forest at the Wind River Canopy Crane site in the southern Washington Cascades, which experiences slightly drier summer conditions than the forests in this study, supports relatively few epiphytic bryophytes and cyanolichens, especially above 30 m (McCune et al. 1997). Old-growth associated cyanolichens, including *L. oregana*, *Pseudocyphellaria rainierensis*, and *Sticta weigelii*, appear to reach their greatest accumulations and widest vertical distributions in the humid Douglas-fir forests of the central Oregon Cascades (pers. obs.).

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Lichens and Mosses on Shrub-steppe Soils in Southeastern Washington

Abstract

The purpose of this study was to identify the lichens and mosses found on soils of the shrub-steppe at the Hanford Site in southeastern Washington. Twelve sites between 133 and 447 m and one at 807 m elevation were intensively sampled. Twenty-nine lichens and six moss species were identified. Three lichens were considered undescribed species. Based on comparison with other studies and herbarium records, we conclude the soil lichen flora of the Hanford Site is substantially different than that of the Great Basin or of the shrub-steppe in Idaho.

Introduction

Throughout much of the Intermountain West, a cryptogamic or microbiotic crust covers some or all of the interspace between vascular plants (Nash, 1996a). The crust is composed of water-stable surface soil aggregates bound by algae, fungi, lichens, and moss (Johansen, 1993; St. Clair and Johansen, 1993).

Soil cryptogams play several roles important to the structure of ecosystems in semi-arid regions (Metting 1991, St. Clair and Johansen 1993). Soil cryptogams can stabilize the soil, reducing wind and water erosion (Metting 1991; Johansen 1993; Eldridge and Greene 1994). They contribute nitrogen (Harper and Pendleton 1993; Jeffries et al. 1992; Evans and Ehleringer 1993) and organic carbon (Johansen et al. 1993) to the soil. Some researchers have found an increase in water infiltration into the soil with cryptogamic soil crusts (Brotherson and Rushforth, 1983). Intact cryptogamic crusts can also enhance seedling establishment in arid ecosystems (St. Clair et al. 1984).

The identification of the taxa of soil lichens and mosses of a particular location is an important first step in understanding their role in structuring ecosystems of the area. In the Columbia Basin, very little work has been done to relate lichen species to their environment, primarily because there has been very little collecting in the area (Ryan 1994). An early effort by Daubenmire (1970) lists 13 lichen species and seven moss species likely to be found in the *Artemisia tridentata-Agropyron* association in Washington. Some of the reported identifications were noted as questionable by Daubenmire (1970), with many of the lichens only known to the genus level. An exhaustive review (Ryan 1994) of work done on the lichens of the Columbia Basin of Washington found that collections have only been made in far eastern counties by Cooke (1955) and in Yakima and Grant counties. About 32 soil lichen species are recognized in the Columbia Basin (Ryan 1994). Recently, McCune and Rosentreter (1995) provided a field key to soil lichens of central and eastern Oregon; they recognize 74 species from alpine to lower elevation shrub-steppe ecosystems including acidic to basic soils. McCune and Rosentreter (1995) indicate that their key will also include most soil lichens in steppe communities in eastern Washington. No reports exist on the soil cryptogam floristics in the *Artemisia tridentata-Stipa comata* association (Daubenmire 1970) nor on the Hanford Site.

The objective of this study was to document the species that constitute the lichens and mosses of the lower elevation soils on the Hanford Site.

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We compare our results on species number and composition with those of previous workers in semi-arid and arid regions of the Great Basin and in the semi-arid shrub-steppe. We discuss range extensions, the percent of species that fix nitrogen, and the effect of soil pH on species composition.

Methods

The Hanford Site (Figure 1) in southeastern Washington has cool wet winters and hot dry summers. Precipitation is greatest in the fall and winter with an annual average of 160 mm at lower elevations (Thorp and Hinds 1977). Soils range from silts to sands (Table 1). Surface soil pH ranges from as high as 8.9 under the canopy of *Sarcobatus vermiculatus* to between 6.4 and 6.9 at higher elevations (Rickard and Vaughan 1988, Bolton et al. 1990, Bolton et al. 1993). Vegetation ranges from undisturbed shrub-steppe dominated by *Artemisia tridentata, Purshia tridentata, Grayia spinosa,* and common bunchgrasses such as *Pseudoroegneria spicata*, *Poa sandbergii*, and *Stipa comata* to disturbed sites dominated by *Bromus tectorum* (Table 1). Vascular plant

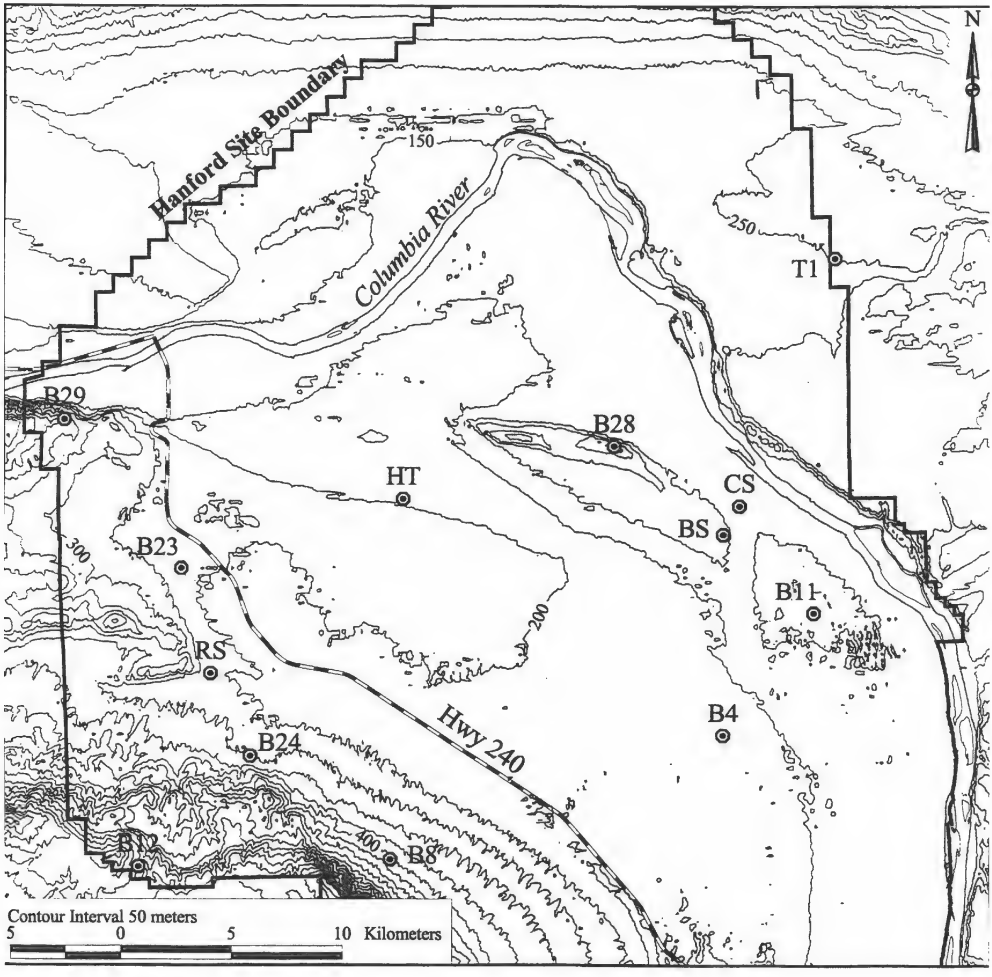

Figure 1. Map of the study sites on the Hanford Site in southeastern Washington. Study site information is presented in Table 1.

TABLE 1. Sample location information on the Hanford Site in Benton and Franklin counties, WA, USA.

Site	Elev. (m)	Soils	Dominant Vegetation
B11	160	Rupert sand	*Purshia tridentata*/Bunchgrass
B12	807	silty loam, loam, sand	*Artemisia tripartita*/Bunchgrass
B23	210	Warden silt loam	*A. tridentata*/*Grayia spinosa* Bunchgrass/*Bromus tectorum*
B24	261	Warden silt loam	*A. tridentata*/Bunchgrass/*B. tectorum*
B28	318	Kiona silt loam	*A. tridentata*/Bunchgrass/*B. tectorum*
B29	447	silty loam, loam, sand	*A. tridentata*/*G. spinosa* Bunchgrass/*B. tectorum*
B4	167	Ephrata sandy loam	*B. tectorum*/*Poa sandbergii*
B8	413	Ritzville silt loam	Bunchgrass
BS	159	Burbank loamy sand	*B. tectorum*/*Poa sandbergii*
CS	186	Burbank loamy sand	*A. tridentata*/*G. spinosa* Bunchgrass/*B. tectorum*
HT	133	Burbank loamy sand	*B. tectorum*
RS	209	Hezel sand	*Sarcobatus vermiculatus*/*P. sandbergii*
T1	268	silt, sand	*P. tridentata*/*A. tridentata*/*Stipa comata* *B. tectorum*

nomenclature primarily follows Hitchcock and Cronquist (1973).

Thirteen sites representative of a range of undisturbed to disturbed plant communities of the lower elevations (133 to 807 m above sea level) at Hanford were sampled (Table 1). Each site was examined by two to six people along a 100 meter transect and collectors were convinced they acquired the entire range of species in a site. Care was taken to prevent the samples from disintegrating because many of the samples were from sandy soils that were not stable.

In the laboratory, specimens were soaked in white glue and water for stabilization, then glued onto 3 x 5 inch cards. They were then cataloged, identified, and placed in lichen/bryophyte packets. Voucher specimens are retained in the herbaria of Arizona State University (lichens) and Washington State University at Tri-Cities (lichens and mosses).

Results

Twenty-nine soil lichens in 19 genera and six moss species in four genera have been identified (Table 2). Twelve (41%) lichen species are of the crustose growth form, eight (28%) are squamulose, seven (24%) are foliose, and two (7%) are fruticose (Table 2).

Three lichen species were previously undescribed. The undescribed *Arthonia* has black apothecia. The undescribed *Trapeliopsis sp.* #1 has a small thallus composed of gray white areoles with black apothecia and the undescribed *Trapeliopsis sp.* #2 has large thalli composed of gray white areoles with orbicular soralia. Two lichen species were identified only to genus level because they were sterile (Table 2). Five (17%) of the lichen species fix nitrogen (Table 2). Two of the six moss species were identified without the aid of fruiting structures and thus are only tentatively named.

Discussion

Our investigation of the floristics of soil cryptogams found on the Hanford Site is the most intensive survey to date in the shrub-steppe of Washington. We compare our results on species number and composition with those of previous workers

TABLE 2. Lichens and mosses occurring on soils of the Hanford Site and in common with other studies. Growth form (c = crustose, s = squamulose, fo = foliose, fr = fruticose), ability to fix nitrogen, and occurrence in other studies [1 - St. Clair et al. (1993), Great Basin (GB), Intermountain shrub-steppe (ISS); 2 - Pearson and Rope (1987); 3 - Rosentreter (1986); 4 - Kaltenecker (1997); 5 - McCune and Rosentreter (1995); 6 - Daubenmire (1970); 7 - Ryan (1994)] are indicated.

	Growth Form	Nitrogen Fixer	1 GB	1 ISS	2	3	4	5	6	7
Lichens										
Acarospora geogena H. Magn.	c									
Acarospora schleicheri (Ach.) A. Massal.	s				•	•	•	•		•
Amandinea punctata (Hoffm.) Coppins & Scheid.	c				•			•		•
Arthonia sp. (undescribed)	c									
Arthonia glebosa Tuck.	c					•		•		•
Aspicilia sp. (*A. calcarea* group) sterile	c			•						
Aspicilia reptans (Looman) Wetmore	s			•			•	•		•
Caloplaca jungermanniae (Vahl) Th. Fr.	c							•		•
Caloplaca tominii Savicz	c		•			•	•	•		•
Candelariella terrigena Rasanen	c					•	•	•		•
Cladonia fimbriata (L.) Fr.	fr							•		•
Cladonia pyxidata (L.) Hoffm.	fr					•				•
Collema cf. *tenax* (Sw.) Ach.	fo	•	•	•	•	•	•	•	•	•
Diploschistes muscorum (Scop.) R.Sant	c						•	•		•
Endocarpon pusillum Hedw.	s		•				•	•		
Lecanora hagenii (Ach.) Ach.	c				•					
Lecanora muralis (Schreb.) Rabenh.	c				•	•	•	•		•
Leptochidium albociliatum (Desm.) M. Choisy	fo	•				•	•	•		•
Leptogium lichenoides (L.) Zahlbr.	fo	•					•	•		•
Massalongia carnosa (Dickson) Korber	fo	•				•	•	•		•
Peltigera rufescens (Weis) Humb.	fo	•				•		•		•
Physconia enteroxantha (Nyl.) Poelt	fo									•
Physconia isidiigera (Zahlbr.) Essl.	fo									
Placynthiella sp. (sterile)	c									•
Psora globifera (Ach.) Mass.	s		•		•		•	•	•	•
Psora luridella (Tuck.) Fink	s		•		•	•			•	•
Psora montana Timdal	s							•		•
Trapeliopsis sp. 1 (undescribed)	s									
Trapeliopsis sp. 2 (undescribed; aff. *wallrothii*)	s									
Mosses	NA	NA	NA	NA	NA			NA		NA
Bryum argenteum Hedw.						•	•		•	
Bryum cf *caespiticium* Hedw. (sterile)									•	
Ceratodon purpureus (Hedw.) Brid.						•	•		•	
Grimmia cf *montana* Bruch. (sterile)										
Tortula papillosissima (Coppey) Brotherus										
Tortula ruralis (Hedw.) Gaertn						•	•		•	

in semi-arid and arid regions of the Great Basin and in the semi-arid shrub-steppe. We discuss range extensions and the percent of species that fix nitrogen. Finally, we discuss the effect of soil pH on species composition.

Species Number and Composition

The recent review of terricolous lichens of the Intermountain Area by St. Clair et al. (1993) describes only 12 species in steppe habitats. Only three species, *Aspicilia reptans, Aspicilia* sp., and *Collema tenax*, occur in both the steppe described in St. Clair et al. (1993) and Hanford (Table 2). In addition, of the 12 species in steppe habitats described in St. Clair et al. (1993), 75% are squamulose or foliose and 25% are fruticose, while in the shrub-steppe at Hanford, 54 % are squamulose or foliose, 7% are fruticose, and 41% are crustose. The soil lichen flora of Hanford is more heavily weighted to the low-stature, crustose, growth form than the soil lichen flora of the steppe described in St. Clair et al. (1993). Only five species were common (Table 2) between our study and the list of 13 for the Great Basin in St. Clair et al. (1993). The 29 species observed in our study suggests that the shrub-steppe at Hanford is very rich in soil lichens compared with other areas of the Intermountain Area. In addition, because so few species are common between Hanford and those also listed in St. Clair et al. (1993) and the difference in growth form distribution, we conclude that the soil lichen flora of the lower Columbia Basin at Hanford is unlike that of the Intermountain Area described in St. Clair et al. (1993).

A survey of lichens at the Idaho National Engineering Laboratory in the shrub-steppe of southeastern Idaho (Pearson and Rope 1987) describes only 7 soil lichen taxa that are in common with those of Hanford (Table 2).

In a study of soil mosses and lichens in the shrub-steppe near Boise, Idaho, Rosentreter (1986) recognized 30 different lichen species. Of these, only 11 were also found at Hanford (Table 2). Rosentreter (1986) also identified six moss species, of which three are in common with those of Hanford (Table 2). In another study of soil mosses and lichens near Boise, Idaho, Kaltenecker (1997) recognized 36 different lichen species. Of these only 14 were also found at Hanford (Table 2). Kaltenecker (1997) recognized nine moss species, of which only three are in common with those of Hanford (Table 2).

On the basis of studies done by St. Clair et al. (1993), Pearson and Rope (1987), Rosentreter (1986), and Kaltenecker (1997) we conclude there is little similarity between the soil lichen and moss flora of Hanford and the soil lichen and moss floras of the Great Basin or of the Idaho shrub-steppe.

Our lichen species list has more in common with the 74 species occurring on soils in central and eastern Oregon (McCune and Rosentreter 1995) than with lichen floras of the Great Basin (St. Clair et al. 1993). Of the lichens identified to species at Hanford, six (Table 2) are not found in McCune and Rosentreter (1995). The large number of species recognized by McCune and Rosentreter (1995) is a result of inclusion of habitats at high to low elevation and of basic to acidic soils. In contrast, the 29 species in our study were found only at low elevations (133 m to 807 m).

In Washington, in areas generally comparable to the Hanford Site, Daubenmire (1970) recognized 13 representative species and genera of soil lichens and mosses, of which only seven species were found in our study (Table 2). A possible reason for this difference is soil substrate. The soils examined in our study ranged from, primarily sands to silts (Table 1) while Daubenmire (1970) describes lichens and mosses found mostly on loamy or stony loam soils.

Range Extensions and the Percent of Species that Fix Nitrogen

An exhaustive survey of herbaria for lichens of Washington revealed all, but five species (Table 2) found in our study (Ryan 1994). We report *Acarospora geogena* and *Endocarpon pusillum* as new records for Washington. The three undescribed species (Table 2) in our report were not reported in Ryan (1994). Some of the undescribed lichen species found at Hanford potentially have been recognized by others (McCune and Rosentreter 1995, Kaltenecker 1997). Giving specific epithets to them will require further analysis by soil lichen taxonomists.

Our findings have extended the known range of the *Cladonia* species to Benton and Franklin counties. *Cladonia fimbriata* has been collected throughout the Pacific Northwest, although less commonly in semi-arid interior regions (Hammer 1995). *Cladonia pyxidata* has not been reported in the semi-arid interior regions of the Pacific Northwest (Hammer 1995). Our findings are in

contrast to the report that *Cladonia* is not represented by a single species in the soil crust communities of the Great Basin or Colorado Plateau (St. Clair et al. 1993).

We found five species (17% of the soil lichen flora) capable of fixing nitrogen at Hanford (Table 2). St. Clair et al. (1993) report only one nitrogen-fixing soil lichen (Table 2) out of 34 species (3%) found in the Intermountain Area. Approximately ten percent of lichens fix atmospheric nitrogen (Nash 1996b). With 17% of soil lichens capable of fixing nitrogen, the soil lichen flora of Hanford appears relatively rich in nitrogen fixing species.

Soil pH

Lichen species composition is influenced by soil pH (Hale 1974, Nash 1996a). Lichens can be used to compute a soil pH index because many species favor acidic soils, while other species favor basic soils (McCune and Rosentreter 1995). McCune and Rosentreter (1995) list ten common species of acidic soils and ten of basic soils. Six of our species (*Acarospora schleicheri*, *Arthonia glebosa*, *Aspicilia reptans*, *Diploschistes muscorum*, *Leptochidium albociliatum*, *Placynthiella* sp.) fall into the acidic soil grouping while only two (*Caloplaca tominii*, *Collema* cf. *tenax*) are in common with the ten listed for basic soils. This confirms observations that the surface soils of the Fitzner-Eberhardt Arid Lands Ecology Reserve on the Hanford Site are slightly acidic with pH values as low as 6.5 (Rickard and Vaughan 1988; Bolton et al. 1990; Bolton et al. 1993; Johansen et al. 1993). Because six out of eight common species at Hanford fall into the acidic soil grouping of McCune and Rosentreter (1995) we suggest that most of the surface soils sampled in our study are slightly acidic. The suggested acidic nature of the surface soils at the Hanford Site is a potential cause for the large differences between species composition of the Hanford Site and the species composition of the Great Basin (St. Clair et al. 1993) that is dominated by basic soils. The differences may be attributed to the sensitivity of species to Al^{3+} (Kershaw 1985) and nutrient levels that are affected by pH (Nash 1996a) such as phosphorus (Bidwell, 1974).

Conclusion

Based on the large differences between our results and those of previous workers we have described a rather unique soil lichen flora for the Hanford Site. Given the limited number of sites and habitats sampled in our study we expect that more species will be recognized with expanded sampling. The soil cryptogam identifications for the Hanford Site in this study have added significantly to our biodiversity knowledge base.

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Relations of Climate and Radial Increment of Western Hemlock in an Old-growth Douglas-fir Forest in Southern Washington

Abstract

The objective of this study was to examine the association of western hemlock (*Tsuga heterophylla*) growth to climate across structural levels in an old-growth forest. The canopy vertical gradient was sectioned into six 10-m height classes with western hemlock growth examined in the top five levels. All trees in a 4.0 ha plot (n = 645), greater than 15cm diameter at breast height (DBH) were cored for the recent 20-year growth record. Growth chronologies representing each height class were correlated to 10 climatic variables. The 40-50m height class exhibited the highest correlations to climate and the 10-20m height class exhibited the lowest. When moving averages of 3 and 5 years were applied to the growth index and climatic variables, the correlations of height class one (10-20m) became the strongest suggesting that growth of canopy dominants is determined by short term climatic conditions while understory growth was influenced by longer term climatic conditions. Understory growth at the 5-year temporal scale was strongly ($-0.6 > R < -0.8$) and negatively correlated to temperature while its correlation to precipitation was strongly positive. The annual depth of snow at the 5-year time scale was the only climatic variable to affect growth similarly for all height classes, indicating consecutive years of deep snow had a negative impact upon western hemlock productivity.

Understanding effects of canopy structure upon the relationships between climate and tree growth can improve interpretation of past climatic conditions and stand dynamics from long tree cores. The climatic signal for stand chronologies that experienced suppression or competition could be adjusted for typical changes that occur with tree ascension to canopy dominance. Current uses of universal climate-growth relationships in forest ecosystems (e.g., gap family models), especially in structurally diverse old-growth stands, provide a questionable picture of forest growth and dynamics.

Introduction

The relationship between the formation of tree rings and climate is well established and can be used to investigate changing stand conditions related to disturbance, stand development or climatic variation (Fritts 1976, Hughes et al. 1982, Fritts and Swetnam 1989, Brakel and Visser 1996). For example, the climatic record of a drought is commonly found in a tree ring series with the formation of relatively narrow rings (Fritts and Swetnam 1989, Cook and Kairiukstis 1990, Lane 1991). However, growth-limiting factors can be interactive and complex depending upon the variation of environment experienced by a given tree through space (canopy position) and time (maturity or age). By measuring and comparing changes in tree ring characteristics sampled along particular ecological gradients we can gain insights into the interaction of climate and stand structure. An old-growth stand provides the ideal vertical depth required for a clear separation of ecological gradients associated with stand structure. However, the complexity of multiple canopy layers and the scale of heterogeneity characteristic of a temperate old-growth rain forest requires intense and large scale tree sampling (Spies et al. 1990).

Most of the unique compositional and functional attributes of old-growth are derived from their structural characteristics. Stand structure in old-growth includes a wide ranges of tree sizes, deep canopies, and abundant dead wood (Franklin et al. 1981, Smith and Long 1989, Franklin and Spies 1991, Tappeiner et al. 1997). Canopy gaps are a main feature of the canopy layers and contribute greatly to the horizontal and vertical complexity that is found in an old-growth forest stand (Oliver and Larson 1990, Lertzman et al. 1996, Song et al. 1997). Structural understory heterogeneity is closely related to, and highly dependent upon, the architecture of the canopy layers (Song 1998). Since complex structural attributes affect ecosystem functions such as growing conditions, we hypothesized that radial growth response would vary depending on the vertical and horizontal position of a tree in the canopy.

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Earlier dendroecological investigations into the role of climate on the radial growth of the forest stand have been limited to analysis of canopy dominants as it was believed that these trees exhibit the clearest climatic signals and contain the longest records (Fritts 1976, Brubaker 1980). Dendroecological investigations into stand dynamics have been avoided in closed canopy systems because the climatic signal in understory trees was thought to be obscured or weakened by the presence of intense competition. Incorrect estimations of the future effects of climate change and the past interpolations of climatic conditions may occur by assuming a uniform response to climate among all height classes. Understanding the effects of stand structure upon tree growth at all levels of the forest canopy will begin to unravel the complex nature of old-growth function. Given these insights and the lack of research in this area, we attempted to reveal the nature of growth rate and climatic relationships at various height levels.

The objectives of this study were to: 1) examine the correlation of climatic variables to the growth of western hemlock from five height classes over a 20-year period. 2) construct predictive models of growth for each height class using climatic variables. 3) examine the correlations between climate and growth among height classes at the larger temporal scales of three and five years. We hypothesized that growth rates of each height class have unique correlations to climatic variables.

Methods

Study Site

The four-hectare study plot is located in the T. T. Munger Research Natural Area at the Wind River Experimental Forest near Carson, Washington. The plot is in the Wind River valley at 355 m elevation, deep within the southern Washington Cascade Range (45.49° N, -121.58° W). It is located on gentle topography near the base of Trout Creek Hill, an extinct volcanic cone. Soils are coarse textured (Shotty loamy sands and sandy loams) Inceptisols developing in two to three meters of volcanic ejecta over basalt bedrock. A seasonally intermittent stream runs through the center of the study site from west to east. The region is characterized by a climate with wet winters, and dry summers. Annual precipitation is 2528 mm with less than 10% occurring between June and September. Average annual snowfall is 2330 mm. Mean annual temperature is 8.7° C. This 500-year-old forest is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Other tree species include western redcedar (*Thuja plicata*), Pacific silver fir (*Abies amabilis*), noble fir (*Abies procera*), and grand fir (*Abies grandis*).

Dendroecological Methods and Data Analysis

A tree's canopy position or relative height defines its physiological maturity better than chronological age (Fritts 1976, Kramer and Kozlowski 1979, Cook and Kairiukstis 1990). Therefore, we defined the ecological gradient for analysis along height classes rather than diameter at breast height (DBH) classes. We obtained estimates of height from tree diameter using a non-linear regression model developed by Song (1998) (Figure 1). We then sorted all tree species into six 10-m height classes. Western hemlock was chosen for analysis since it was present in all height classes (Table 1). Height class 2-10m was not core sampled and not included in any analysis. The remaining height classes one, two, three, four, and five represent trees with heights ranging from 10-20m, 20-30m, 30-40m, 40-50m, and 50-60m respectively. Height classes one, two, three, four, and five contain n = 175, 124, 111, 164, and 59 trees, respectively.

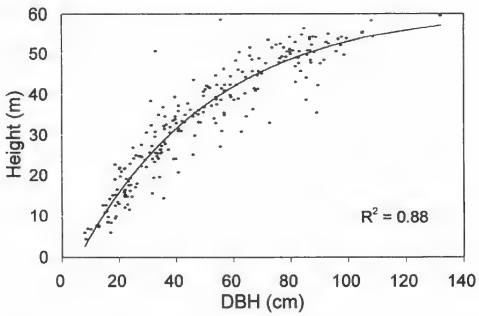

Figure 1. Non-linear regression relationship of western hemlock DBH and height. Model (*Height* = 61.50949137 – 69.5364329 * $e^{(0.02108786 \cdot DBH)}$) has a r^2 = 0.88. Model developed by Song (1998).

We took one increment core from the north face of each live western hemlock tree >15 cm at 1.37m or higher (n = 645) in the 4 hectare study plot. A second core 45 degrees from the first was

TABLE 1. Height class frequency distribution (trees per hectare) of major tree species in an old-growth Douglas-fir forest near the Wind River Canopy Crane research area in south central WA.

Height Class	Pacific silver fir	grand fir	Western red cedar	Douglas-fir	Pacific yew	western hemlock
2-10m	34		4		105	93
10-20m	7	1	2		10	49
20-30m	2	2	1		1	30
30-40m		4	2	1		28
40-50m		2	2	6		42
50-60m		1	1	21		14

taken from 26 trees that had obvious physical damage to the bole face or a rotted core. We took core samples 4-7 cm in length in order to capture at least the last 20 annual growth rings. We sealed the cores in numbered plastic straws and stored them frozen to prevent rotting, breaking, and cracking. We mounted thawed cores on grooved boards for sanding and ease of measurement following the techniques set forth by Stokes and Smiley (1968).

Crossdating is a procedure that insures that each ring increment is placed in its proper time sequence (Fritts 1976). A common crossdating technique is to match ring width patterns in one ring series with ring patterns in an established site chronology. This method was not applied due to the short growth record collected, and lack of conspicuous marker years or width patterns. Crossdating techniques employed in this study consisted of careful inspection of the core samples for signs of false and missing rings (Stokes and Smiley 1968). Samples exhibiting the characteristics of a false ring were removed from the analysis (n = 12). Missing rings, usually due to stress from climate or other factors, can fail to show an early-latewood pattern entirely and must be compared to other samples for confirmation (Stokes and Smiley 1968). Since a site chronology was not established and direct comparison was not possible, missing rings may be present and misrepresenting the true ring series. A recount and comparison of 20% of the core samples was performed in order to insure proper measuring technique and prevent measuring errors such as misalignment of ring widths, inaccuracy, and imprecision. It is assumed that the quantity and intensity of the sampling will average the dating errors caused by only taking one core per tree and not crossdating to a site chronology.

Tree ring widths vary with fluctuations in the environment and systematically with changes in tree age and height. Standardization is required to correct ring widths for the changing age and geometry of the tree; transformed values are ring-width indices (Fritts 1976). Van Deusen (1987) introduced a method of standardization, named "differencing", that requires little subjectivity and can be used to process large numbers of cores automatically.

$$\text{Log}\,[R(t)] - \text{Log}\,[R(t-1)] = \Delta\text{Log}\,[\text{R(t)}] \qquad (1)$$

Where: R = growth increment, t = time (year)

This method creates a first difference by taking the difference of natural log transformation of the growth increment of one year from the previous year. The log transformation puts the ring series on a relative scale. The first difference is a first derivative that can be viewed as a growth rate. The resulting index has a mean of zero and is the relative rate of change in ring width from one year to the next (Van Deusen 1987). Comparing two trees of differing sizes, ages, and growth rates before and after standardization indicates that these effects are removed (Figure 2a and 2b).

For the final step in the data transformation, we averaged the detrended tree ring indices in each height class for each year to produce height class chronologies. This averaging removes the effects of local disturbance, random error and amplifies the climatic signal desired for analysis (Fritts 1976, Cook and Kairiukstis 1990, Van Deusen 1990). To insure that the effects of outliers did not influence the variance and bias of the mean a biweight robust mean procedure, with five

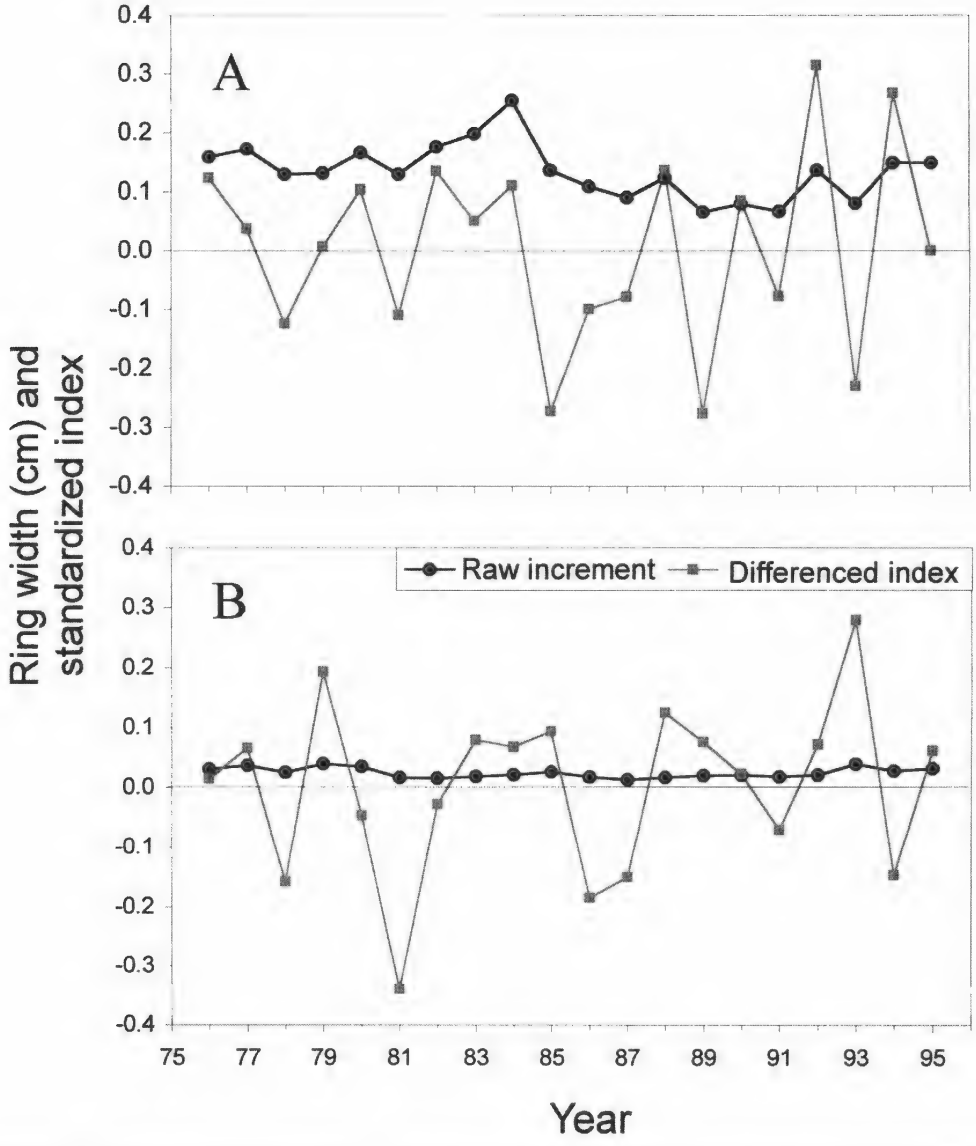

Figure 2. Comparison of standardization effect upon two increment cores from different canopy levels. Standardization effect upon a vigorously growing western hemlock single tree ring series (tree #4374) from the fourth height class (40-50m)(A). Standardization effect upon a complacent or suppressed single western hemlock tree ring series (tree #5156) from height class one (10-20m) (B).

iterations, was used to obtain the final chronologies (Cook and Kairiukstis 1990). The biweight mean procedure was also used to average the raw ring series data for each height class to compare the effects of the standardization and observe ring characteristics within each height class (Figure 3). The comparison of transformed data or chronologies (Figure 4) illustrates the resulting stan-

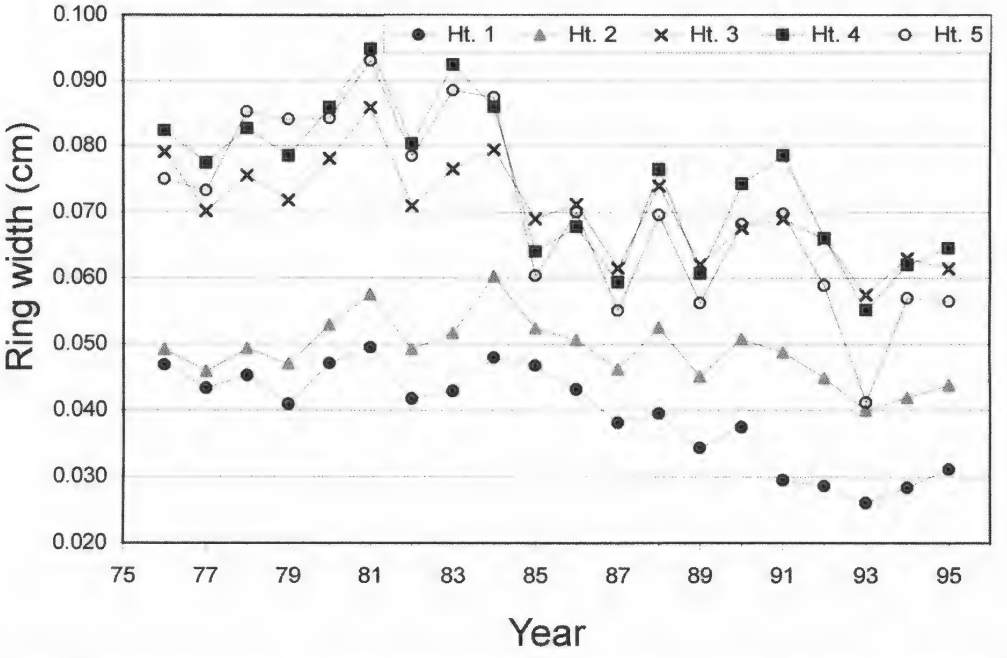

Figure 3. Biweight means for each height class of western hemlock for a 20-year increment record. Data are not transformed and represent actual ring increment widths.

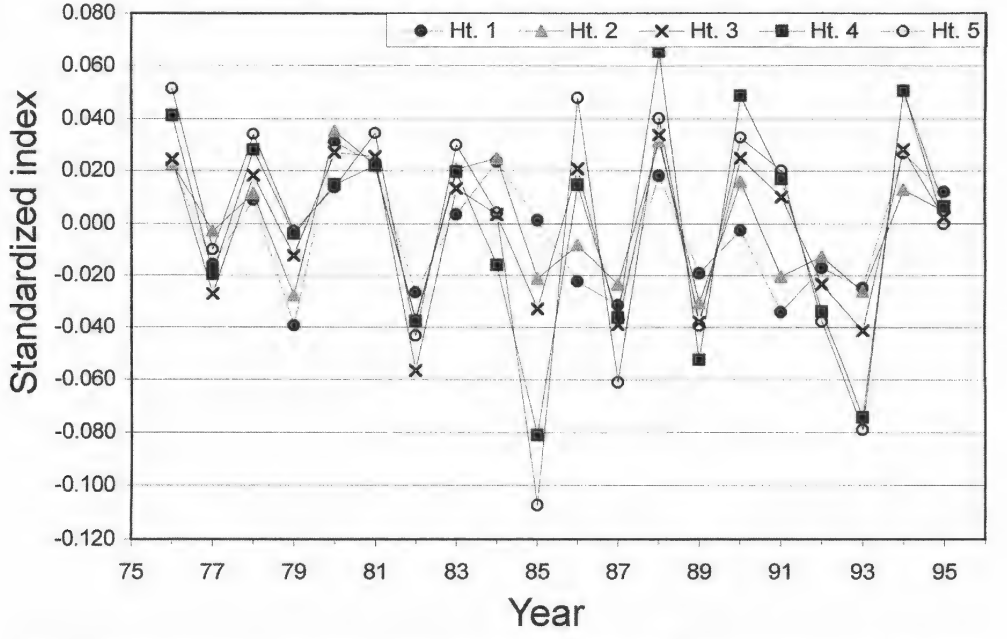

Figure 4. Chronologies for five height classes of western hemlock for a 20 year record. Data are transformed using the standardization technique of "differencing."

TABLE 2. Climatic variables chosen for analysis with height class growth data.

Variable	Description	Rationale
PT9-11	Mean temperature and precipitation September, October and November. Means of parameters were multiplied	These two variables were combined to reveal any interactive effects that may not be revealed in multiple regression techniques. Other combinations of temperature and corresponding precipitation were also investigated, but failed to produce a result of at least intermediate strength ($\|R\| > 0.4$ in any height class).
T9-11	Mean temperature September, October and November	Warmer temperatures during this period may serve to extend the growing season, especially when combined with the termination of the summer droughty season. An extension of favorable conditions for growth should translate into continued photosynthetic activity and cambial expansion.
P9-11	Mean precipitation of September, October and November	The summer dry climate of the Pacific Northwest results in low soil moisture in late summer and reaches its extreme in August. While preliminary investigation revealed poor correlation between summer (July through September) precipitation and growth, the later precipitation during September through November did correlate with growth. Improved soil water status late in the growing season may act to extend the growing season and continue cambial activity and growth.
T7-9	Mean temperature of July, August, and September	Warmer temperatures accelerate cambial cell division and cell expansion is sensitive to warmer than average temperatures during the period of cambial activity. Warm temperatures during this period should enhance the radial increment by increasing rates of cambial activity, cell expansion and photosynthesis (Brubaker et al.1992).
T2-4	Mean temperature of February, March and April	Photosynthetic rates increase in response to rising air and soil temperatures in the spring. Early spring temperature should combine the direct effects of air temperature on photosynthesis as well as the indirect effects of snow melt on the physiological activity of trees (Brubaker et al.1992).
T4	April temperature	See "T2-4".
AT	Mean annual temperature	This variable was retained to provide a baseline of comparison to the aforementioned variables and because of its own significance over the 20 year period
AP	Mean annual precipitation	This variable was retained to provide a baseline of comparison to the aforementioned variables and because of its own significance over the 20-year period.
AS	Mean annual depth of snow	Depth of snow is known to negatively effect growth rates of trees in the Cascade Mountains (Brubaker et. al. 1992; Ettl and Peterson 1995). Deep and lingering snows can delay the onset of cambial activity and hence reduce the growing season.
P-PT9-11	Previous year mean temperature and precipitation September, October and November. Means of parameters were multiplied.	Since it is usually assumed that biological processes cause growth in one year to influence growth in subsequent years, a lag effect from an increased growing season should positively effect the shoot and cambial predeterminism of the subsequent year (Fritts 1976; Hughes et al.1982; Kramer and Kozlowski 1979). Increased photosynthesis late in the growing period may not prolong cambial activity but may instead be stored as simple carbon for the following season. Lag effects for all variables were investigated while "P-PT9-11" was best correlated to tree growth variability.

dardization upon the height class robust means. All regressions and correlations were done using these transformed chronologies.

The choices for the climatic variables (Table 2) are a combination of pre-defined models and correlation analysis. Pre-defined models or variables that have demonstrated effects on growth in past studies restricted the variables entering the analysis to biologically relevant variables that are expected to affect growth (Brubaker et al. 1992). The minimum daily temperature, maximum daily temperature, average daily precipitation and average daily snowfall were obtained for cooperative station #451160 Carson Fish Hatchery (45.54^0 N -121.51^0 W Elev. 345m) and cooperative station #459342 Wind River (45.48^0 N -121.56^0 W Elev. 351m). The data from the Carson Fish Hatchery covered 1977-1996 and data from the Wind River station covered 1975-1976. To fill data gaps of one or two days, we used averages of previous and following days. We filled larger data gaps (whole months) with regression outputs based on regional climatic data. Less than 1% of the climatic data was estimated. We constructed climatic variables by sorting month(s) and parameter(s) of interest and averaging over 20 years. To investigate lag effects of the growth-climate we correlated growth in year *t* with climatic variables from year *t*-1.

The relative correlation strengths of chronology to each climatic variable were determined using Pearson's correlation analysis. Absolute values of correlations to each climatic variable were averaged to obtain a mean correlation for each height class. Moving averages were applied to the climatic variables and used to examine longer wavelengths or lag effects in tree growth-climate relations (Douglas 1936, Fritts 1976). The 3-year moving average removes trends shorter than three years and is used to determine which climatic variables have a long-term influence upon the growth rate differences. Used in a similar fashion, the 5-year moving average affords a longer perspective on the chronology-climate relationships. Pearson's correlation analysis was performed between chronologies and each climatic variable after application of the three and 5-year moving averages.

Multiple linear regression analysis was conducted using SAS and the best final regression models were chosen using two procedures (SAS Institute 1989). The "all possible regressions" procedure was used to choose the best model for growth prediction. The best model or "goodness of fit" was determined with the adjusted coefficient of determination (adj. r^2), and a model bias estimate based on the total mean squared error (Mallow's Cp) (Neter et al. 1996). Stepwise regression, with an entry/exit threshold of P=0.15, was the second technique for choosing the best model. Friedman's test was used to determine whether the correlations for all climatic variables were equal across height classes. Since correlation data for height classes three, four and five failed the Shapiro-Wilks' W test for normality (P=0.008, 0.005, and 0.018, respectively), a nonparametric test was used (StatSoft, Inc 1998). The Wilcoxon matched pair signed rank test was used to investigate significant differences in correlation of growth rate to climatic variables between all pairs of height classes (StatSoft, Inc 1998).

Results

Results of the statistical analysis are separately described in order of Pearson correlation temporal scales followed by regression models selection and nonparametric tests. Chronology correlations without application of a moving average is strongest in the 40-50m height class with a mean correlation of $|R| = 0.37$, and reaches its lowest mean correlation of $|R| = 0.13$ in the 10-20m height class (Table 3). Correlation to "AS" reveals negative correlation for all height classes with the highest correlations from the 50-60m height class (Figure 5a). Height class one shows no correlation ($|R| < 0.2$) to temperature variables (T9-11, T7-9, T4, T2-4, AT) and weak correlation ($0.2 > |R| < 0.4$) to the remaining precipitation variables. While the sign of the Pearson correlations are evaluated,

TABLE 3. Absolute value means of all Pearson correlations (|R|) between climatic variables and western hemlock chronologies by height class.2

Height Class	10–20m	20–30m	30–40m	40–50m	50–60m
Mean correlation	0.13	0.23	0.27	0.37	0.34
Mean correlation of 3-year averages	0.44	0.35	0.14	0.29	0.21
Mean correlation of 5-year averages	0.62	0.46	0.25	0.35	0.22

its strengths are considered as absolute values. The 20-30m and the 30-40m height classes are most similar in their correlation response to climatic variables resulting in similar means (0.23 and 0.27 respectively) (Figure 5a). Height class five (50-60m) is moderately correlated ($0.4 > |R| < 0.6$) to variables PT9-11, AT, and AS.

The application of the 3-year moving average dramatically increases correlation strengths for height class 10-20m well into the moderate range ($0.4 > |R| < 0.6$) for all climatic variables except AS and P-PT9-11 (Figure 5b). The negative correlation response by both the 10-20m and the 20-30m height classes are similar for all temperature variables. For remaining height classes three, four, and five, correlation strengths decline for nearly all other comparisons of climate and growth. Means of the 3-year average climatic correlations indicate that those for the 10-20m height class are strongest and those for the 30-40m height class are weakest (Table 3).

The correlations from the 5-year moving average are strong ($0.6 > |R| < 0.8$) for the 10-20m height class for all climatic variables except PT9-11, T2-4, and P-PT9-11 (Figure 5c). Similar to the 3-year moving average the 10-20m and 20-30m height classes are negatively correlated to all temperature variables and have positive correlations to precipitation variables. Strong correlations to AS are found for all height classes except at 40-50m, which was of moderate strength. AS is the only climatic variable which all height classes are compatible in correlation sign and strength (Figure 5c).

Multiple linear regression models indicate the 10-20m height class is least correlated to climate for both model selection procedures (Table 4). The 40-50m height class has the highest coeffi-

TABLE 4. Coefficient of determination (r^2) for each multiple regression modeling approach by height class. "Stepwise" is an automated approach in SAS (SAS institute 1997), "Adjusted r^2/Cp" is selecting the model with the combined most favorable output total. The "Full model" is the output with all ten climatic variables included.

Height Class	10–20m	20–30m	30–40m	40–50m	50–60m
Stepwise	0.19	0.29	0.27	0.38	0.45
Adjusted r^2&Cp	0.16 / 0.06*	0.22 / 0.13*	0.21 / 0.12*	0.38 / 0.31*	0.37 / 0.30*
Full model	0.25	0.35	0.36	0.51	0.46

* Adjusted r^2 of regression model.

TABLE 5. The climatic variables included for two approaches to multiple regression modeling, stepwise selection and an integrated Adjusted r^2 and Cp approach, are given for each height class of western hemlock. Climatic variable definitions can be found in Table 2.

	Height Class									
Climatic	10–20m		20–30m		30–40m		40–50m		50–60m	
variable	Stepwise	Adj. r^2/Cp	Stepwise	Adj. r^2/Cp	Stepwise	Adj. r^2/Cp	Stepwise	Adj. r^2/Cp	Stepwise	Adj. r^2/Cp
PT9-11			X	X			X	X	X	
T9-11					X	X			X	
P9-11	X	X			X	X				
T7-9							X	X		
T4	X		X	X						
T2-4										
AT			X				X	X		
AP										
AS			X	X					X	X
P-PT9-11	X	X			X				X	X

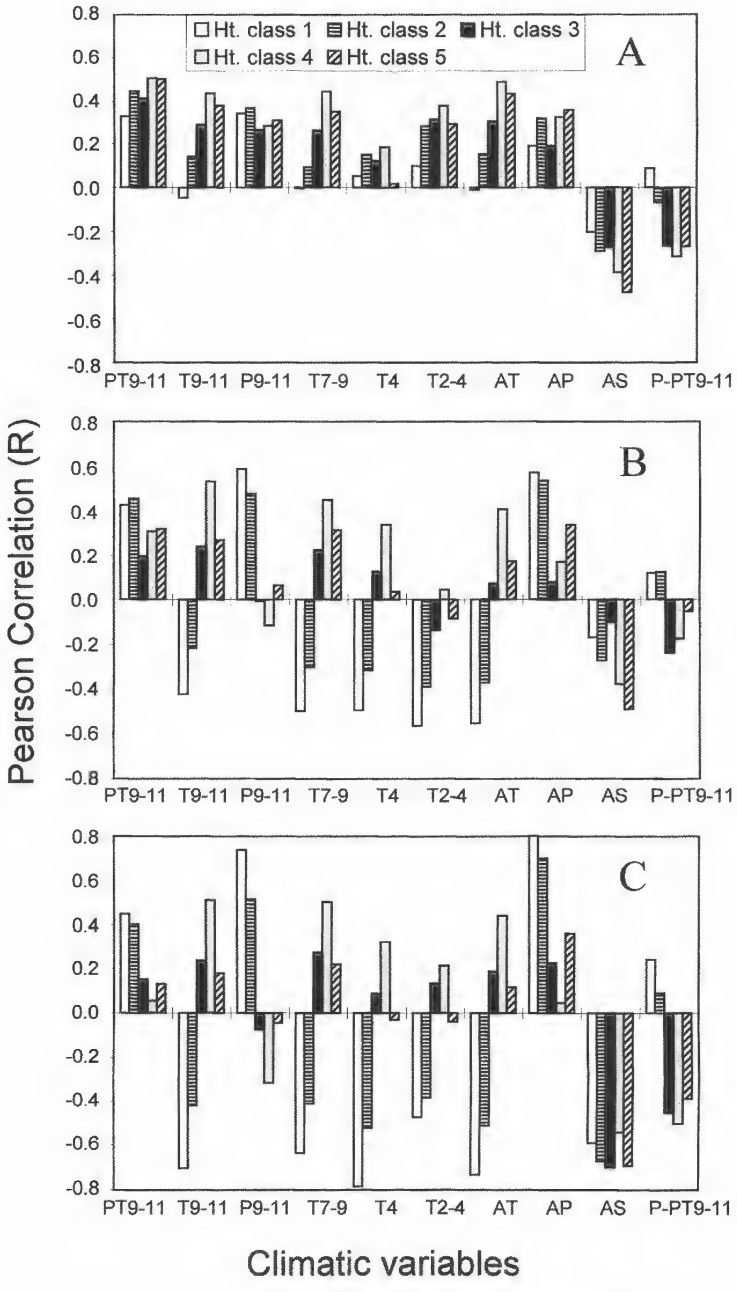

Figure 5. Pearson correlations (R) between climatic variables and western hemlock chronologies by height class. Correlations without an applied moving average (A). Correlations after application of a 3-year moving average (B). Correlations after the application of a 5-year moving average (C).

TABLE 6. Wilcoxon signed rank test significant difference (*P*-value) for each pairing of height classes. Test if height class pairing correlations to climate are unique.

	Height class			
Height class	10–20m	20–30m	30–40m	40–50m
20–30m	0.06			
30–40m	0.28	0.98		
40–50m	0.14	0.28	0.05	
50–60m	0.28	0.58	0.45	0.06

cient of determination with the adj. r^2 & C_p selection procedure while the 50-60m height class has the best model using the stepwise procedure (Table 4). The two selection procedures selected most of same climatic variables for the best models (Table 5). No single climatic variable was chosen for all height classes, regardless of selection procedure, although temperature or precipitation variables during the autumn months (PT9-11, T9-11, P9-11, P-PT9-11) are present in all height classes.

The correlations between chronologies and climate are significantly different (Friedman's nonparametric test, $P = 0.0003$) among the five height classes. The Wilcoxon signed rank test comparing all possible pairs of chronologies for differences in correlation to climate indicate a few pairs are significantly different (Table 6). The Wilcoxon test comparing the 20-30m and 30-40m height classes indicate they are the least different ($P = 0.98$) in their correlation to the ten climatic variables.

Inspection of raw data statistics shows that the 40-50m height class contains the greatest mean ring increment, maximum ring increment, standard deviation, and variance (Table 7). Smallest mean ring widths, standard deviations, and variances were all found in the lowest two height classes.

Discussion and Conclusion

Our results show the growth rates of western hemlock trees present in each height class have a different response to climate. The Wilcoxon test revealed that adjacent height classes, with the exception of height classes two and three, were significantly different in their correlation to climatic variables. Significant differences in adjacent height class correlations support the notion that each has a unique relationship with climate and represents a separate ecological gradient. The Pearson correlations reveal the relative differences in correlation strength to each climatic variable while the regression models determine which combination of climatic variables best predict a change in growth. Strengths of the climatic growth correlations to canopy dominants in this study were similar to those reported by others in the region (Brubaker 1980, Brubaker et al. 1992, Peterson and Peterson 1994, Ettl and Peterson 1995). The raw data show differences of growth rates between height classes and are consistent with the notion that understory trees have reduced growth rates (Figure 3) (Table 7).

To understand the relationship of growth to climate we can view the results by height class, variable season (spring, summer etc.), variable type (temperature and precipitation), temporal scale (3-year and 5-year moving averages) or combinations of the above. For the suppressed trees in height class one, the striking result of the mov-

TABLE 7. Summary statistics for raw ring widths (mm) of western hemlock, by height class.

	Height Class				
Parameter	10–20m	20–30m	30–40m	40–50m	50–60m
N of rings	3500	2480	2220	3280	1180
Mean (cm)	0.066	0.075	0.108	0.120	0.105
Median (cm)	0.049	0.063	0.091	0.104	0.099
Minimum (cm)	0.004	0.001	0.006	0.006	0.016
Maximum (cm)	0.447	0.303	0.584	0.848	0.714
Sample variance	0.0031	0.0025	0.0059	0.0067	0.0034
Standard deviation	0.0558	0.0496	0.0769	0.0820	0.0582

ing average indicates that these trees were most affected by longer term trends in the climate (Figure 5c) (Table 3). The presence of T4 in only the first two height class regression models indicates that spring temperatures are important but the strong negative relationship of growth to temperature was only revealed with longer time scale analysis. The canopy dominants were most affected by short term climatic trends; correlation strength decreased as the time scale of analysis increased (Table 3). The notable exception to this short-term correlation trend for height class five was the climatic variable AS to which ring widths were moderately or strongly correlated for all time scales (Figure 5). The annual depth of snow affects growth for all height classes at the 5-year time scale showed that consecutive years of deep snow have a negative impact upon all western hemlock productivity. The presence of autumnal climatic variables in the regression models (PT9-11, T9-11, P9-11, P-PT9-11) of all height classes suggests these climatic conditions also influence productivity across the entire stand.

It appears that as tolerant trees such as western hemlock pass through structural levels in the canopy they experience different relationships to climate. Hence, the resulting ring series have widths with a complicated history of causation. Current dendrochronological practices avoid stands and trees that experienced suppression or treat the relationships to climate uniformly along a tree ring series. Understanding what climatic variables have the most effect upon growth at a given height class has the potential to reveal past climatic conditions recorded in large old-growth trees and aid in the understanding of recruitment dynamics.

Future studies might include similar analysis of other species in the same stand to provide insight into their ecology and better illustrate the complete stand dynamic. Finally, this study illustrates the need to preserve the remaining old-growth because there is still much unknown about the dynamics and complexity of these systems.

Acknowledgements

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Some Effects of Urbanization on Streamflow Records in a Small Watershed in the Lower Fraser Valley, B.C.

Abstract

Times series of monthly, mean daily and maximum instantaneous streamflows were examined for changes which may be associated with urbanization within the Nicomekl watershed in the lower Fraser Valley of British Columbia, Canada. An adjacent watershed, the Salmon which has had much less urbanization, provided a comparison. In these low lying watersheds which receive heavy winter precipitation even slight increases in runoff could lead to increased flooding problems. Urbanization is relatively new in this area and though land use changes due to urbanization are not yet extensive, statistically significant increases in streamflow were detected. Continued urbanization causing increased runoff may generate increased flooding problems in the future.

Introduction

As Hipel *et al* (1977) have pointed out, a major challenge in hydrology is the detection, modeling, and description of the effects of man-induced or natural interventions, or alterations, on time series of hydrologic variables. In this study of two streams in the lower Fraser Valley of British Columbia, Canada, the intervention is change in landuse and landcover brought about by urbanization. The time series of hydrologic variables considered were monthly streamflows, annual maximum daily flows, and annual maximum instantaneous flows.

At the time of European arrival, the lower Fraser Valley was densely forested. At present what forest remains is second or third growth. European settlers established agriculture as the predominant landuse. As Moore (1990: 1) states, "Some of Canada's most important agricultural land and wildlife habitat is located in British Columbia's Lower Fraser Valley." Since 1970, the population of Greater Vancouver has been increasing rapidly and the effects of this increase are propagating into the Lower Fraser Valley. Moore (1990) indicates that between 1981 and 1986 the Lower Fraser Valley had one of the fastest growth rates in Canada (9.1%). The Lower Fraser Valley is a confined area, with mountains to the north and east, Georgia Strait to the west and the International Boundary with the United States of America to the south.

In this confined area, the effects of urban development have become a significant concern. The effects of urbanization upon hydrology has become a subject of worldwide concern (International Workshop on Integrated Water Resources Management in Urban and Surrounding Areas, 1994). A first step towards the assessment of the effects of urbanization upon the hydrology of a basin is the examination of the available streamflow data to ascertain whether there are detectable changes that may be related to urbanization (McCuen and Thomas, 1990). Exploratory data analysis techniques are used in our study, and as Eagleson (1979) pointed out, our results are not general as they do not incorporate climate, soil, and vegetal properties. This study is intended as an initial step in examining the effects of landuse change using more generalized water balance models. Intervention modeling of these data is reported in Leith and Whitfield (1996).

Data Assembly and Methods

Assembly of a time series of streamflow data that spans urbanization of a basin was difficult as hydrometric stations in British Columbia routinely have been discontinued when a basin suffered sufficient alteration (intervention) that the flow was deemed to have been changed from the "natural" regime. Fortunately, the Nicomekl River,

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which flows through the City of Langley, has records before and during intense urbanization. There are streamflow records from an adjacent basin to the east, the Salmon River, and a major tributary of the Nicomekl, Murray Creek available for comparison. The geographical arrangement of the basins is shown in Figure 1. Table 1 provides the hydrometric station names, identifiers, and periods of record.

Three measures of urbanization are used in this study: census data, building permits, and air photos. Population data for Langley City and Langley District are plotted in Figure 2 and estimates of landuse and landcover made from air photos are summarized in Table 2. These estimates were made by delineating the drainage basins on air photos taken in 1967 and 1982. Each basin was divided into 1-kilometer squares, and each square was

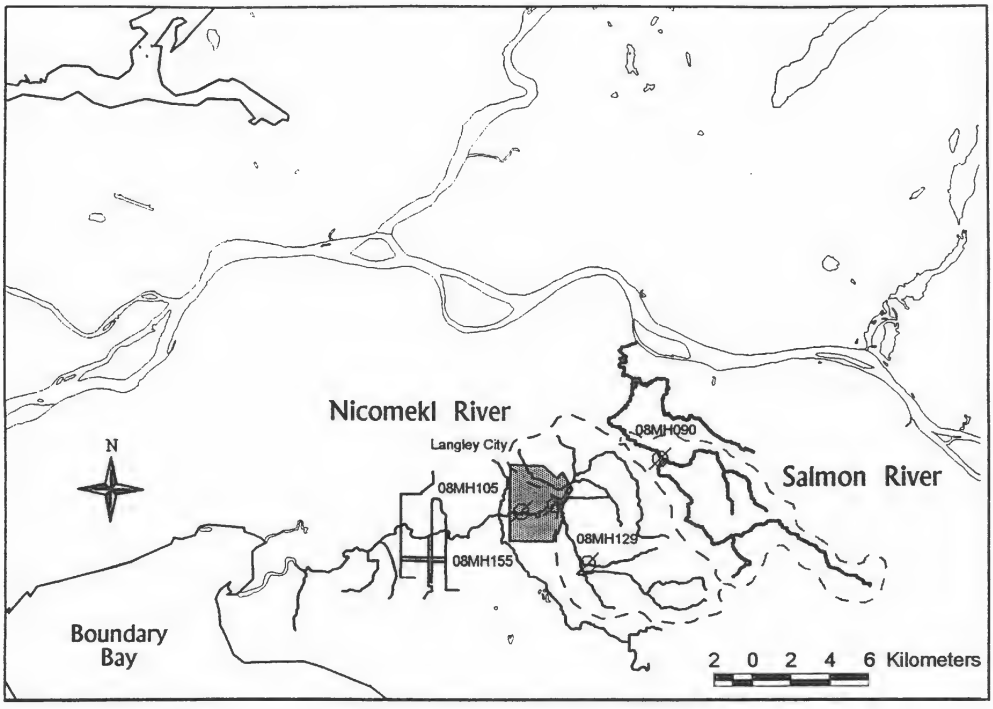

Figure 1. Location of the Nicomekl and Salmon basins in the lower Fraser Valley to the southeast of Vancouver. The Fraser River is shown to the north. The station identifiers are referenced in Table 1.

TABLE 1. Hydrometric Stations in Nicomekl and Salmon Watersheds.

Water Survey of Canada Station Identifier	Station Name	Drainage Area (km^2)	Period of Operation
08MH105	Nicomekl River below Murray Creek	64.5	April 1965–October 1984
08MH155	Nicomekl River at 203 Street, Langley	69.2	February 1985–present
08MH129	Murray Creek at 216 Street, Langley	26.2	March 1969–November 1983
08MH090	Salmon River at 72 Avenue, Langley	49	February 1960–September 1964 December 1968–present

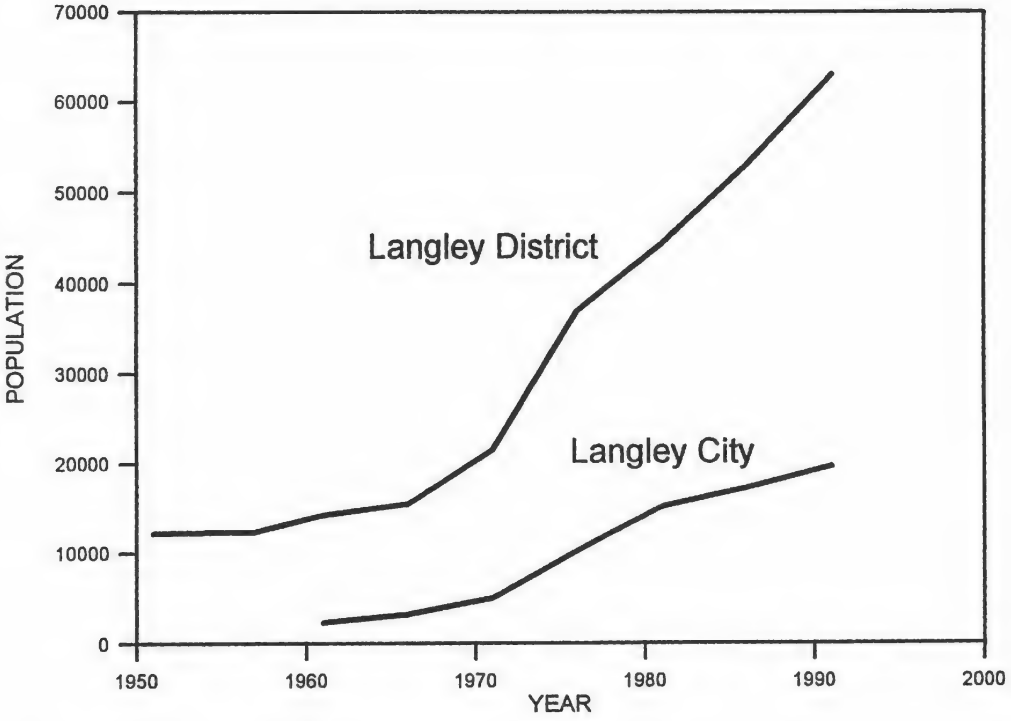

Figure 2. Population growth in Langley City and Langley District between 1950 and 1990.

TABLE 2. Landuse and landcover in the study area in 1967 and 1982.

	Nicomekl Basin			Murray Basin			Salmon Basin		
Year	Forest	Agric.	Urban	Forest	Agric.	Urban	Forest	Agric.	Urban
1967	34%	64%	1%	44%	56%	0%	51%	46%	3%
1982	24%	68%	8%	34%	63%	3%	34%	58%	7%

classified according to the predominant land use land cover within the square.

Monthly runoffs from the Nicomekl River below Murray Creek (08MH105) gauging station were plotted against monthly runoff from the Salmon River. Runoff is the volume of streamflow discharge over a period of time divided by the drainage area of the basin. Using runoff as the hydrologic response adjusts for differences in drainage areas. Monthly runoffs from two time periods, the first 1968-1972 before intense urbanization and the second 1980-1984, during and after intense urbanization were compared. The start of the intense urbanization was estimated from the rate of population increase, Figure 2, and the peak in building permits in 1979 and 1980. Air photos were available only in 1967 and 1982 so the beginning of rapid increase in urbanization could not be estimated from this data.

To produce homogeneous independent sequences, seasonality and serial dependence were removed from the Nicomekl and Salmon River monthly runoffs. Seasonality was removed by subtraction of the appropriate monthly mean (i.e. we subtracted the overall July mean from each July value) and serial dependence was removed using the lag one correlation coefficient (i.e. the correlation between one month and one follow-

ing). The result of this is to produce a series which has no seasonal pattern and no auto-correlated structure. Regression equations were developed for the 1968-1972 and the 1980-1984 periods. These equations were then tested to determine if the regression parameters were statistically distinct.

Maximum Daily and Maximum Instantaneous flows for the Nicomekl, Salmon, and Murray were input to a Flood Frequency Program, Kite (1991). Ten year floods, i.e. peak flows with a return period of ten years or a probability of exceedance less than or equal to 0.1 in any year, together with 95% confidence intervals were estimated for 2 parameter log normal and 3 parameter log normal distributions. Estimates were made by maximum likelihood and the method of moments. The 10-year flood was investigated, as five to eight observations were available so the extrapolation is small.

In November 1984, the gauging station on the Nicomekl River below Murray Creek (08MH105) was closed and in February of 1985, a station was relocated down stream to 203 Street, Langley (08MH155). To ascertain whether changes were brought about by the relocation of the gauging station, the observed peak flows from the new station were adjusted by the drainage area ratio (64.5/69.2) so that they could be compared with data from the previous location.

Results and Discussion

From the analysis of air photos the increase in urban area for the Nicomekl basin from 1965 to 1982 was 7%, 3% of which was in the Murray Creek tributary. The remaining 4% was largely concentrated in the City of Langley. The urbanization in Murray Creek was mainly small distributed housing developments, while in the City of Langley urbanization consisted of large housing developments, light industrial activity, and extensive parking lots in a concentrated area.

TABLE 3. Regression Coefficients for deseasonalized and deserialized monthly runoffs.

Time Period	Regression Coefficient	Probability
1968–1972	1.037	<0.01
1980–1984	1.144	<0.01

In the Salmon basin, urban area increased 4%, mostly small housing developments distributed throughout the watershed. The forest cover was reduced by 17%, so the Salmon basin has had landcover changes during the study period. Thus, it was not a static control. Table 3 provides the regression coefficients for the deseasonalized deserialized Nicomekl monthly runoffs as functions of the deseasonalized deserialized Salmon monthly runoffs. The intercepts were not significantly different from zero.

From an F-test, the regression coefficients are significantly different from each other at the one percent significance level. The change in slope indicates an increase in the monthly runoffs for the Nicomekl River relative to the Salmon River, as indicated in Figure 3.

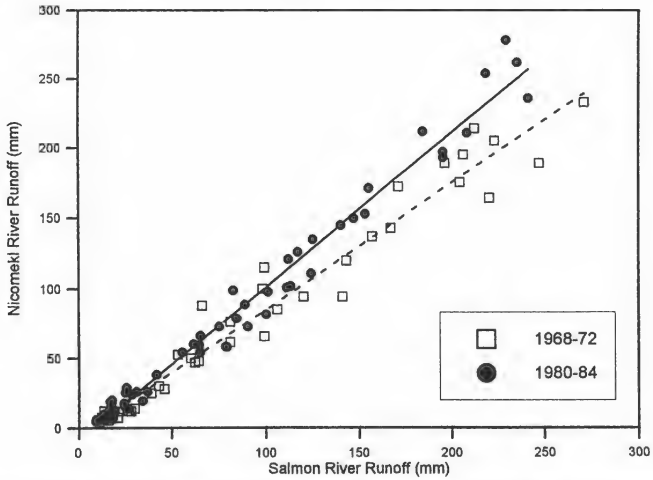

Figure 3. Relationship between monthly runoffs for Salmon and Nicomekl Rivers before intense urbanization (1968-72) and after (1980-84).

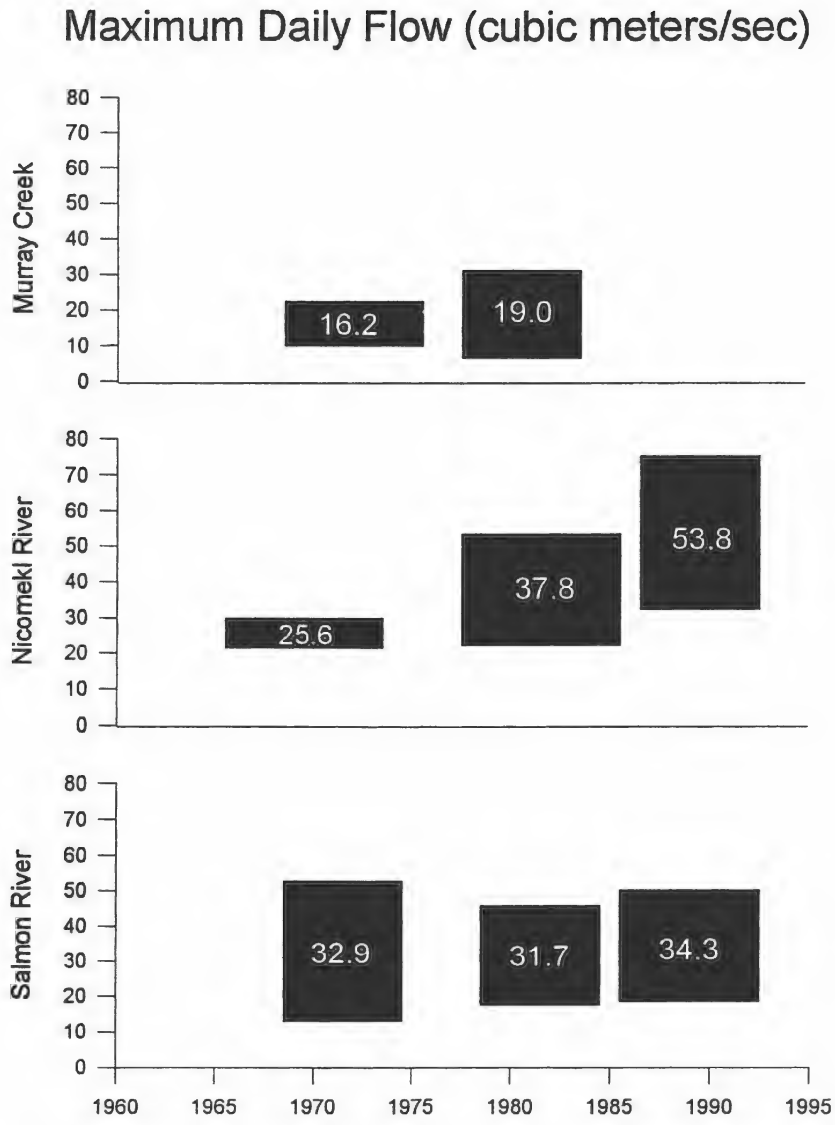

Figure 4. Estimates of 10-year maximum daily flood for Murray Creek, Nicomekl River, and Salmon River over the period of urbanization. The estimated flood is indicated by the number in the bar, the width of the bar gives the time period for data used in making the estimate and the vertical length of the bar shows the 95% confidence internal for the estimate.

From sequences of maximum daily flows, estimates of 10 year floods made using the two parameter log normal distribution are shown in Figure 4. The vertical bars in Figure 4 provide 95% confidence intervals with the estimated 10 year floods shown in numerals within the bar. Results for the three parameter log normal distribution were similar to those of the two parameter and are not shown. For Murray Creek, the estimated 10 year flood does not change significantly between the periods 1969-1975 and 1978-1983. The Nicomekl River below Murray Creek shows a significant

increase from 25.6 cubic meters per second (cms) in 1968-1972 to 37.8 cms in 1978-1984. After the gauge was relocated, there was a marginally significant increase to 53.8 cms. The estimated flood for the Salmon River does not change significantly for any of the periods 1968-1972, 1978-1984, and 1985-1992.

Considering maximum instantaneous flows, the Salmon River does not show any significant change in the estimate of 10 year flood, Figure 5. The Nicomekl River (08MH105) shows no change to 1984, but the 1984 maximum instantaneous flow is missing and the 1984 maximum daily flow is the highest on record. In the period 1985-1992

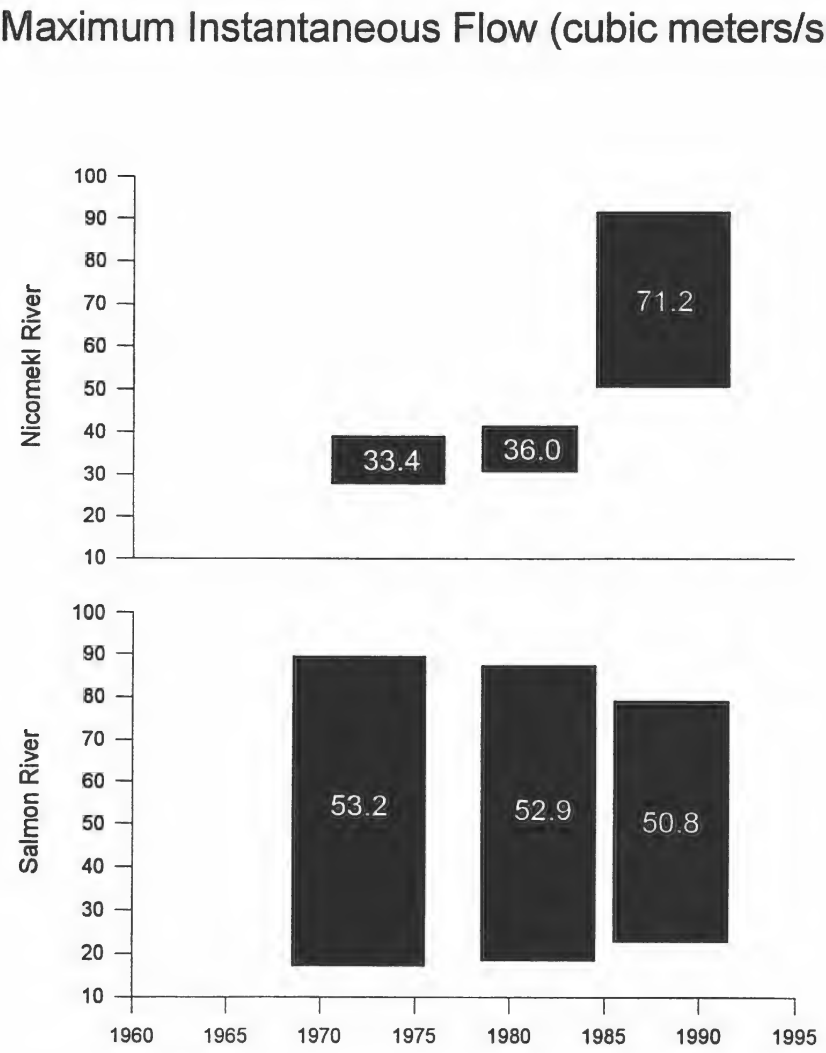

Figure 5. Estimates of the 10-year maximum instantaneous flood for Nicomekl River and Salmon River over the period of urbanization. . The estimated flood is indicated by the number in the bar, the width of the bar gives the time period for data used in making the estimate and the vertical length of the bar shows the 95% confidence internal for the estimate.

there is a significant increase in the estimate of 10 year maximum instantaneous flood.

Despite the adjustments to flows to account for the increase in contributing area, moving the gauge on the Nicomekl River has significantly altered the maximum daily and maximum instantaneous flows. The area added to the basin, although small, is intensely urbanized including parking lots and commercial development.

Conclusions

In the Nicomekl drainage, there have been significant increases in monthly stream flow and 10 year maximum instantaneous flood since 1967. These changes have occurred at the same time as intense urbanization in concentrated areas within the basin. Although there has been some development in the Murray Creek and Salmon River basins there does not appear to have been significant changes in maximum daily or maximum instantaneous flows in these basins. The distributed nature of urban growth in these basins is thought to be the fundamental difference from the Nicomekl basin. The changes to the Nicomekl flow regime have taken place in that part of the basin, which does not include Murray Creek. These results suggest that even a small amount of concentrated urbanization can significantly alter flow regimes.

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Notes

The purpose of "Notes" is to periodically publish short papers (typically less than five pages in length). There is no specific format or content required for articles published here, but all papers will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.

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Polar Plotting of Seasonal Hydrologic and Climatic Data

Abstract

A polar plot form for visualizing changes in seasonal data is presented. This representation treats time as a cyclical variable and removes the winter year-boundary discontinuity created by standard Cartesian plotting methods. Polar plots facilitate visual presentation of changes in the magnitude and phase of environmental variables and allow effective visualization of seasonal patterns. Examples of polar plots are presented using streamflow data from two streams in British Columbia. This method is particularly useful for comparing and contrasting systems that exhibit different patterns of seasonal shifts.

Introduction

The need for improved methods of presenting complex scientific information has been recognized in the statistical literature for some time (Fienberg, 1979). When scientific results are presented to both technical and non-technical audiences, as is often the case in the environmental sciences, this need is especially strong. Recently, formal procedures for identifying effective graphical methods have been proposed (Cleveland and McGill, 1984; 1987). They show how certain graph types can be better than others at presenting certain types of information.

Traditionally, the direction, magnitude, and significance of changes and trends in environmental data have been reported via results from hypothesis tests. As pointed out by Loftus (1993), the graphical presentation of experimental data offers a more effective way of communicating this information to an audience. Overlaying time-series plots of environmental variables (i.e. hydrographs for presenting changes in discharge) is one means of graphically presenting this type of information (e.g. Leith and Whitfield, 1998). However, time-series plots do have drawbacks. These methods can obscure observed changes and make graphical comparisons between different systems difficult. We present a method developed to better illustrate impacts of climate variations on environmental systems. This method is particularly useful for illustrating changes in the phase and magnitude of seasonal variables.

Method

We will illustrate the effectiveness of this presentation method using changes in discharge in streams in British Columbia as an example. Leith and Whitfield (1998) and Whitfield (2000) have shown that the magnitude and timing of runoff events in streams in British Columbia have changed over recent decades. Onset dates of hydrologic spring and fall in streams in south-central B.C. are occurring earlier in the year. From our research perspective, we also deal with coastal streams where the highest discharges are during the winter and lowest during summer.

Traditional hydrographs from two streams in British Columbia during two recent decades are shown in Figure 1. Peak flows from the snow melt driven Tulameen River (at Princeton) occur in spring and summer while peak flows from the rainfall driven Sarita River (near Bamfield) occur

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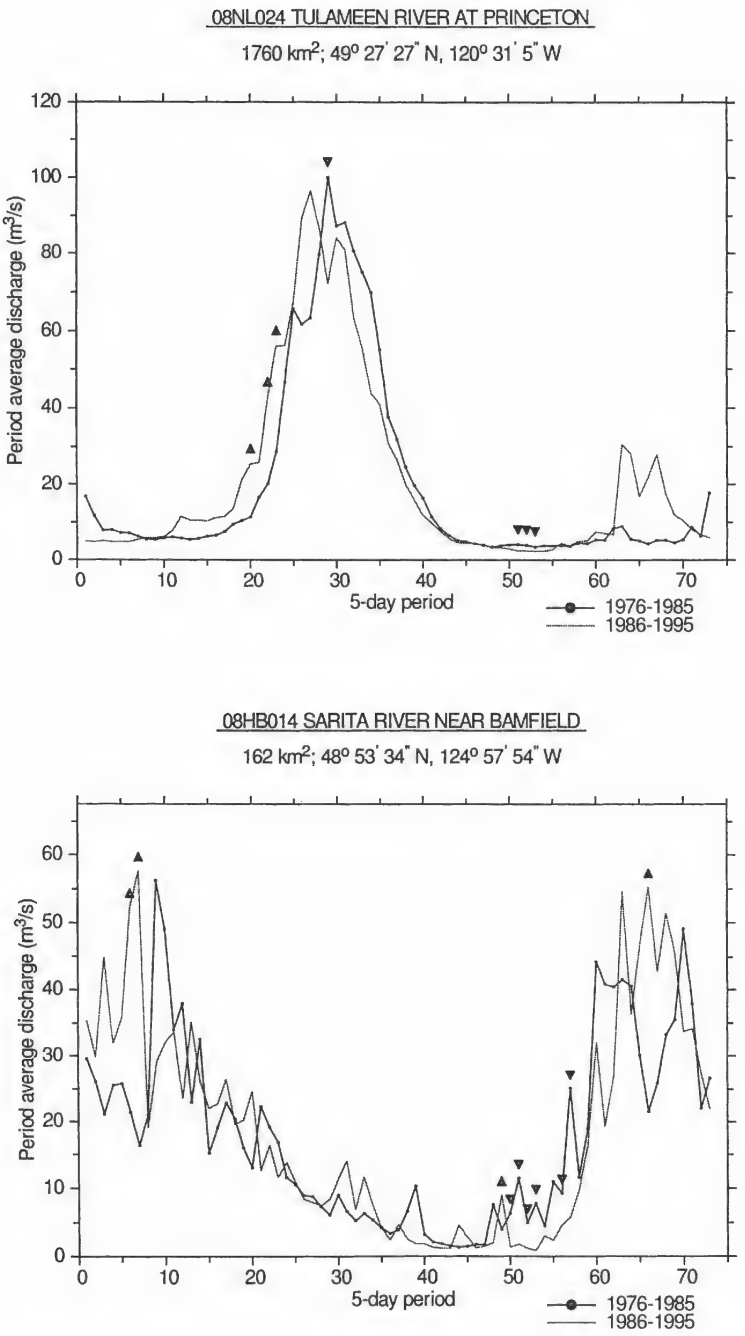


Figure 1. Discharge hydrographs for the Tulameen River at Princeton and Sarita River near Bamfield. Discharge values are decadal means of 5-day averages.

during winter. Arrowheads on each graph indicate periods during which changes in flow between the two decades are statistically significant ($p < 0.05$). Leith and Whitfield (1998) present details of the statistical methodology. The Tulameen River exhibits earlier spring flows and an earlier summer low-flow period; the Sarita River exhibits increases in winter and decreases in summer.

By treating time in a linear fashion, the hydrograph imposes an artificial break in discharge across the winter year-boundary (December-January). Visually, we have found that this discontinuity can be confusing when trying to compare shifts in cyclical variables, such as discharge, which peak at different times of the year. In Figure 1, changes in peak flows that occur in winter, such as those observed in the Sarita River, are de-emphasized when they are split between the two ends of the plot.

We have developed a polar plot form for presenting information on changes in magnitude and phase of seasonal variables. The polar plot form we present treats time in a cyclical fashion. This removes the year-boundary discontinuity and facilitates visual presentation of shifts in magnitude and phase of environmental variables.

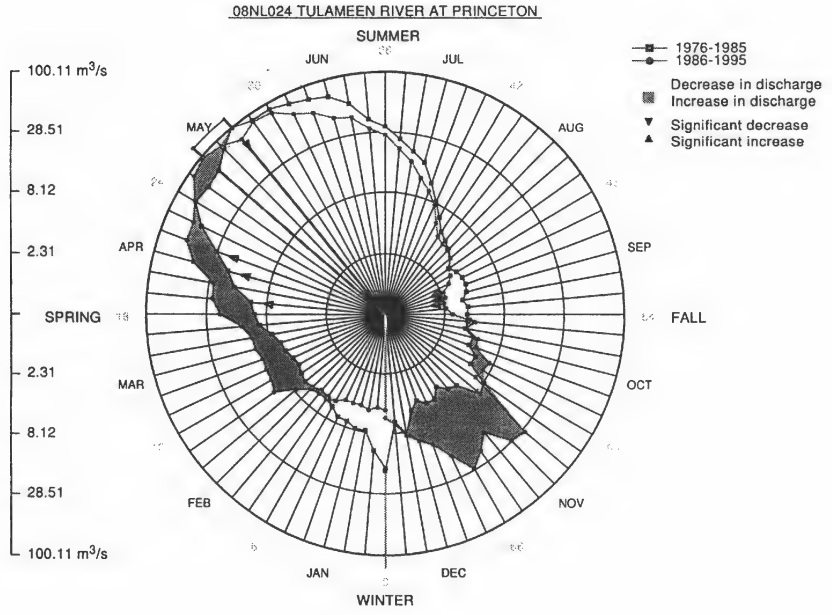
Polar plots of the two hydrographs shown previously are given in Figure 2. The rules used to construct these plots are:

1. The beginning of the calendar year is located at the bottom of the graph.
2. The time interval t_i of the data is converted into degrees by $360(t_i - t_{min})/(t_{max}-t_{min})$. The interval of data is indicated by the number of lines, and the names of the calendar seasons are applied for the reader's benefit.
3. The maximum and minimum of the data is determined and used to set the values of the outer ring (maximum) and the inner ring (minimum). The vertical scaling may be either linear or logarithmic.
4. The two data series are plotted, each shaded differently.
5. The area between the curves is shaded dark when the second curve is larger, light when the second curve is smaller.
6. Significance arrows are attached to the curves. If the second curve is significantly larger then a light-shaded up arrow is located on the radial line indicating the time period; if significantly smaller then a dark-shaded down arrow is applied.
7. The time period of the maximum for each data set is determined and a shaded radial line is drawn indicating each period. An arc is then drawn between the two peaks.
8. A vertical bar indicating the vertical scaling is placed to the left, and other details of annotation are applied as appropriate (i.e. station name and numbers).

The essential features of this graphic are:

1. The cyclical view shows the timing of the seasons and shifts between calendar time and ecological time.
2. Differences in discharge between time periods are shaded.
3. Periods exhibiting statistically significant changes are marked with arrowheads. The direction of the arrowheads indicates whether the significant trends are increasing or decreasing.
4. A shaded radial line shows the peak in each decade. An arc between the lines indicates the amount and direction of the shift in the peak.
5. The axis on the left shows the range of values observed at the station; the outer ring is the maximum value, and the inner ring is the minimum value.

Data are plotted with a common temporal scale and a scaled discharge scale to facilitate comparison between systems. Shapes and attributes of multiple polar plots showing different systems can be compared and contrasted quite easily as a result. Plotting with polar coordinates uses direction, angle, and length of the plotted rays and arcs to convey information on the timing and magnitude of discharge events. Use of shading emphasizes the types of changes (increases and decreases), and the area between curves gives an indication of the relative size of changes. The addition of arrows denoting significance of changes allows results of statistical tests to be integrated with graphical cues showing actual magnitudes of observed changes. While similar information could be portrayed on a traditional hydrograph, the visual discontinuity between December and January would still be present.



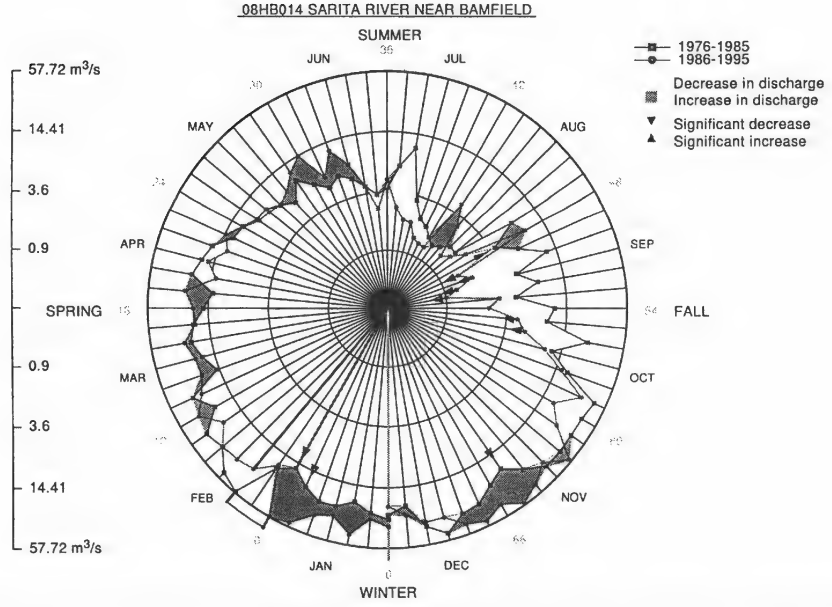


Figure 2. Polar plot representations of the discharge hydrographs shown in Figure 1. Discharge values are log scaled.

This form of graph allows effective communication of changes in discharge both within a given system and between different systems. Direct comparisons between systems are possible and effects of the winter discontinuity are no longer present. While our examples were chosen to compare differences between decades, the methodology could also be used to compare more than two time periods or sets of data. Depending on the number of data sets, multiple shading patterns could be introduced to account for the different relationships between the curves and sets of arrows could be plotted to portray results from the multiple comparisons in the statistical tests.

Conclusion

While polar plots are not new, the application we present here is a useful form to present seasonal hydrologic and climatic data. Our experience has been that plots of the type we have developed allow effective communication with both technical and non-technical audiences.

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Book Reviews

Indians, Fire, and the Land in the Pacific Northwest

Robert Boyd, Editor. Oregon State University Press, Corvallis, Oregon, 313 pages. ISBN 0-87071-459-7 ($34.50)

Forty years ago, the prevailing view of the relationship of Indians, fire, and the land was that "...it would be difficult to find a reason why the Indians should care one way or another if the forest burned...it is quite something else again to contend that the Indians used fire systematically...yet this fantastic idea has been and is still put forth time and again" (Clar 1959). Twenty years ago, the revisionist approach had taken such hold that Pyne (1982) claimed that the fire regime of the Olympic Mountains and the entire Northwest was shaped by anthropogenic fire. Neither the "no fire" nor "all fire" scenarios were supported by any real data; what the debate needed was a definitive source explaining the role of Indian fire in the Pacific Northwest, specific to the landscapes in which the tribes lived. At the turn of the millennium, that source at last has arrived.

Indians, Fire, and the Land is an edited volume containing twelve chapters authored by authorities in the field of history, anthropology, and ecology, with an introduction and conclusion by the editor, Robert Boyd. Chapter authors include Stephen Arno, Stephen Barrett, Theresa Ferguson, David French, Eugene Hunn, Leslie Johnson, Jeff Lalande, Estella Leopold, Henry Lewis, Helen Norton, Reg Pullen, William Robbins, John Ross, Nancy Turner, and Richard White. This impressive list includes anthropologists, historians, and ecologists, and the chapters flow remarkably well. Few of the typical inconsistencies between chapters in edited books are found in this volume, although clearly the authors did not closely collaborate. The chapters include a range of new and previously published material spanning the last forty years of the millennium. Most of the previously published material has been revised for this volume, a nice touch. The chapters range from northern California to British Columbia, and summarize nearly everything that is known about Pacific Northwest Indian use of fire in the environment.

The Introduction effectively summarizes the geographic variation within the region with brief coverage of the "ecoregions". Boyd links the various chapters to these ecoregions. The material is presented chronologically, with the new material comprising the latter chapters. This is a very logical organization, placing the spatially variable chapters into a clear temporal sequence. Some of the previously published material was available through rather obscure outlets, so its reprinting here with revision is quite helpful for an interdisciplinary audience. As a fire ecologist, I found each chapter to be a useful bookmark for future reference.

The argument about whether Indians were part of the "natural" ecosystem or apart from it is a semantic quagmire left for the reader to decide. Indian culture did significantly influence the landscapes of the pre-European contact era, yet this influence varied across the Pacific Northwest. Destruction of native cultures invoked substantial ecological change. Some minor errors in references to plants remind the reader that this is an interdisciplinary volume. Dwarf mistletoe is referred to as an "epiphyte;" Oregon ash (*Fraxinus latifolia*) is called *F. pennsylvanica* (green ash, an East Coast species); and *Poa pratensis* is identified as a bunch grass. The errors I found were few and will not be very significant to most readers.

The concluding chapter is a sobering reminder of the importance of Indian burning to the character of the lands that modern culture usurped from native culture. Was the native way best? Perhaps, the volume concludes, but all of us now exist in a different culture, not native, not European, but North American. Boyd wisely cautions that we may not be able to understand the native ways, or whether or not Indian burning encouraged ecosystem characters such as biodiversity. Yet this volume gives us the state of current understanding so that we may insert our own cultural biases. *Indians, Fire, and the Land* is the most valuable resource to date on Indian burning in the region, and should provide valuable evidence for every reader for his or her next campfire debate.

It should be equally usable by archeologists, anthropologists, ecologists, and historians. This is more than a "recommend"—buy this one—you need it for your library.

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Sunrise to Paradise: The Story of Mount Rainier National Park

Ruth Kirk. 1999, University of Washington Press, Seattle, Washington, 152 pages. ISBN: 0-295-97770-1, cloth; 0-295-97771-X, paper. ($40.00 cloth, $22.50 paper)

I started reading this book during a flight from Seattle on a crisp autumn day. As the plane banked and headed southeast, the upper 3,000 m of Mount Rainier, freshly dusted with new snow, came into view, rising above the clouds like an island in the sea. The mountain truly dominates the physical landscape of the state of Washington, as well as the psychological landscape of many of its residents.

This has been a big year for The Mountain, as locals refer to it, because Mount Rainier National Park is celebrating its 100th anniversary as a national park. Among a handful of new books issued concurrent with the centennial, *Sunrise to Paradise: The Story of Mount Rainier National Park* is the glossiest and best prepared. It is essentially a description of how Mount Rainier National Park interfaces with the history of western Washington.

Sunrise to Paradise is divided into three major parts. In Part 1, author Ruth Kirk does an admirable job of describing the fascinating glaciology and volcanic geology of Mount Rainier. Decades of research and recent scientific publicity have made residents of western Washington increasingly aware that the dynamic physical processes of the mountain are still at work. Several mudflows of past millennia have traveled all the way to Puget Sound, and they will occur again in the future. The figures and narrative in this section are excellent. The rest of Part 1 describes the flora and fauna far too briefly to provide much useful information for readers interested in the natural history of the park. Integration of scientific information in the rest of the book is accurate but sparse.

Part 2 describes the establishment and development of Mount Rainier National Park, with emphasis on the first half of the century. The fifth national park in the United States National Park System, the early evolution of Mount Rainier was similar to that of the other early parks. This is where Kirk excels in describing early Park Service activities, road building, and the development of lodging and recreational facilities for early park visitors. This section is absolutely packed with historical facts and tidbits. Did you know that Mount Rainier National Park was the first park to allow automobiles (in 1907)? Or that there was a golf course (built in 1931) below Paradise Inn?

Part 3 describes the history of human culture at the park. The extensive description of Native American activities and culture in the Mount Rainier region is interesting and informative, and provides a good context for the dramatic and less sustainable wave of Euro-American culture that would follow. The early and more contemporary adventures of hikers and climbers make for an interesting narrative. This section, like the others, is peppered with short essays and interviews about personal experiences of recreationists and former employees. These essays were generally too nostalgic and romanticized for my taste.

The illustrations and photographs in *Sunrise to Paradise*—280 in all—are magnificent. The historical black-and-white photographs were carefully selected to add visual appeal to the book. The layout and editorial condition of the book are excellent. Missing is a photo of a jam-packed parking lot at the popular subalpine destination of Paradise on a summer weekend. The book fails to address the significant management challenges facing park managers today, namely the impact of increasing numbers of visitors and vehicles, and encroaching urbanism on park resources. This was a missed opportunity to discuss an important social issue that will become more prominent in the decades ahead.

Sunrise to Paradise is an interesting and well-illustrated account of the first century of Mount Rainier National Park. Part history book and part coffee-table book, it will hold the attention of Mount Rainier aficionados and history buffs more than scientists.

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Salmon Without Rivers: A History of the Pacific Salmon Crisis

Jim Lichatowich, Island Press, 317 pages. ISBN 1-55963-360-3 ($27.50)

The destruction of salmon habitat in the rivers of the Pacific Northwest started with the near annihilation of the beaver in the last half of the 19th century and continues to this day with the vast software-driven housing explosion of the Puget Sound Basin. *Salmon Without Rivers* is a marvelous effort by a knowledgeable fishery scientist and policy maker to come to grips with the Pacific Northwest salmon crisis from an historical perspective. In my view it is a must-read for anyone with an active interest in the issue of Pacific Northwest salmon as well as anyone interested in the documentation of the history of one of the most important environmental issues of our time.

The essential questions are raised in the first paragraph of the book. Why have the salmon presented the Pacific Northwest with such an intractable problem and why have we been unable to arrest their slide toward extinction and begin rebuilding their populations to some part of their former abundance? The source of the answers to these questions lies in the realization that, contrary to much popular belief, the problem of Pacific Northwest salmon is not a recent one. It has a long history going back more than a a century and a half. And it reflects a vision of nature, based on flawed assumptions and unchallenged myths, that we can control and manipulate the biological productivity of salmon and even improve upon natural processes that we clearly do not understand. In Lichatowich's words, we "assumed we could have salmon without rivers."

The book is divided into three parts. The first part (two chapters) describes the evolutionary history of salmon and the development of the Northwest Indians' gift economy, which was largely based on salmon.

The second part (five chapters) describes the effects of the Euro-American industrial economy on salmon. It starts with a chapter on the two conflicting economies, the natural economy where survival and reproduction are measures of success and the industrial economy where the accumulation of capital and production are measures of success. The next three chapters examine how the industrial economy and its world view destroyed Pacific Northwest salmon through habitat degradation (fur trapping, mining, timber harvest, grazing, irrigation, and hydro-development), rampant over-harvest and waste, and hatcheries (the ultimate form of having your cake and eating it too). The final chapter deals with the issue of science and salmon management, and how numerous scientifically-based opportunities for change in salmon management were lost. In Lichatowich's view, the fundamental assumption of salmon policy since the 1930s has been that "hatcheries could make salmon compatible with fully developed rivers and degraded ecosystems."

The final part of the book (three chapters) deals with the future - first by contrasting approaches to development and management in the two great salmon rivers of the Pacific Northwest (Fraser and Columbia) and showing that institutional structure can make a difference, then documenting recent (last 20 years) developments in the issue (The Road to Extinction), and finally proposing how we might change the story of the past 150 years (Building A New Salmon Culture).

The message in this book is very clear. Over the past 150 years we have consistently assumed that it was possible and desirable to maintain abundant populations of Pacific salmon by simplifying, controlling, and circumventing the ecological processes that created them. In fact the salmon's current state is not the result of a failure of our vision and our management programs; it is the consequence of their success. Our vision has been to make significant progress toward full development of rivers and their surrounding landscape while at the same time employing technology to eliminate the need for rivers to produce salmon. The only way out of this bind is to change our vision and act on it. We must develop a culture capable of nurturing the salmon by finding ways to pay attention to the land and water we share with salmon. In Lichatowich's view, the lesson is clear: if the habitat is available, connected and healthy, the salmon will take care of recovery themselves. We simply cannot have salmon without healthy rivers, estuaries and oceans. And until we carefully examine our core beliefs and assumptions about nature, our rivers, and our salmon, and change our deeper motivations, salmon man-

agement efforts and their institutional Lords of Yesterday—hatcheries and harvest—will continue to threaten the existence of the species they are supposed to protect.

Lichatowich presents a forceful, compelling and moving argument—one that should occupy the forefront of Pacific Northwest public policy as we enter the new millennium. This book needs to be read carefully by scientists, policy makers and citizens who have any interest in preserving salmon as the natural icon of our region. He makes a strong case for radical change in the way that we interact with nature. Rather than attempting to "bend the salmon to our world view" as we have done for the past 150 years, and at the same time ripping their natural tapestry to shreds, we should find ways to pay attention to the land and water we share with salmon. We must begin to seek a balance between the natural and industrial economies in the Northwest. After all, as Lichatowich eloquently points out, with each small population that disappears, with every run that becomes extinct, biodiversity—the very quality that has enabled the salmon to withstand ice ages, mountain uplifts, lava flows, changing ocean conditions, and the whole onslaught of the industrial economy—is lost. Tragically, it is this biodiversity that habitat destruction, overharvest, and the technology of hatcheries have systematically whittled away for over 100 years. If the Pacific salmon are to survive, they will need all of their evolutionary biodiversity that remains. And they will need healthy rivers where that biodiversity is nurtured and maintained. My hat is off to Jim Lichatowich for a job well done.

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Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten in 12 point type on 8-1/2 x 11 inch paper, double-spaced throughout (including abstract, acknowledgements, literature cited, tables, and legends for figures); ample margins must also be provided. The format and style of manuscripts should conform to general usage in recent issues and should consist of sections in the following sequence:

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Journal articles

Broadbooks, H. E. 1970a. Home range and territorial behavior of the yellow pine chipmunk *Eutamius amoenus*. Journal of Mammalogy 51:310-326.

_____. 1970b. Populations of the yellow pine chipmunk, *Eutamius amoenus*. American Midland Naturalist 83:472-488.
Cêska, A., and H. Romer. 1971. A computer program for identifying species group. Vegetatio 20:48-73.
Grizze, J. E., C. F. Starmer, and G. G. Kuch. 1969. Analysis of categorical data by linear models. Biometrics 25:489-504.

Monographs or books

Jennings, H. S. 1906. Behavior of the Lower Organisms. Columbia University Press, New York, USA.

Papers in proceedings or symposia

Ryland, J. S. 1975. Parameters of the lophophore in relation to population structure in a bryozoan community. Pages 363-393, *In* H. Barnes (editor) Proceedings of the 9th European Marine Biology Symposium, Aberdeen University Press, Aberdeen, UK.

Theses, dissertations, personal communications, and articles in press

Donald, D. B. 1971. The limnology of the plankton of three temporary pons in Alberta. M.S. Thesis, University of Calgary, Calgary, Alberta
Wiser, H. C. 1961. Decomposition and homogeneity of continua on 2-manifolds. University of Utah, Salt Lake City. Ph.D. Dissertation.
Dunwiddie, P. W. *In Press*. Dichotomous key to conifer foliage in the Pacific Northwest. Northwest Science.

Technical Bulletins

Daubenmire, R., and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. Washington Agricultural Experiment Station Technical Bulletin Number 60. Washington State University.
Goodwin, J. G., Jr., and C. R. Hungerford. 1979. Rodent population densities in pine forests. USDA Forest Service Research Paper RM-214. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

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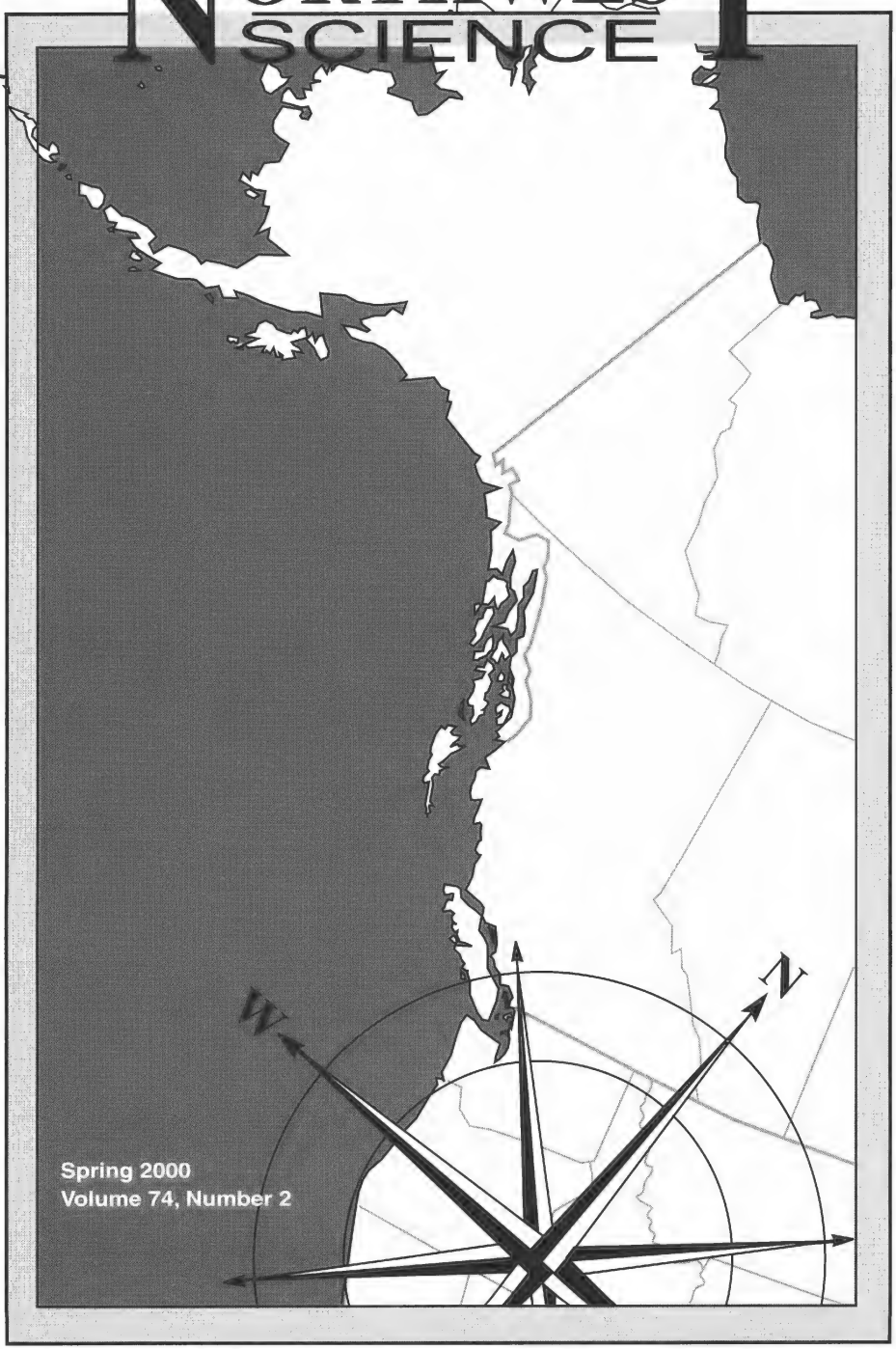

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Announcements

Year 2000 Honorary Life Member and Outstanding Scientist Awards

The two following honorees were awarded with special recognition on March 17, 2000 at the 73rd Northwest Scientific Association Annual Meeting, held in Moscow, Idaho.

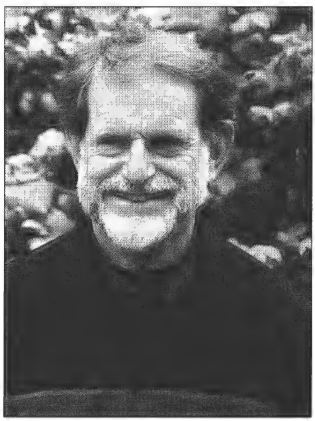
David H. Hansen

Treasurer, Northwest Scientific Association
Honorary Life Membership

It is with pleasure and thanks that Northwest Science Association awards David Hansen with an Honorary Life Membership. He has been treasurer of the Association for over a decade, beginning in 1989. His experienced judgments in presiding over the financial well-being of the Association have been much appreciated. Further, he has brought continuity, dedication, and a longstanding perspective to his participation in executive board meetings and the overall activities of the Association. We sincerely appreciate his efforts and hope that this Honorary Life Membership might serve to convey our sincere thanks to David Hansen for his enthusiasm and devotion to Northwest Science Association.

John C. Tappeiner

Outstanding Scientist



Dr. John C. Tappeiner is highly deserving of the Northwest Scientific Association Outstanding Scientist Award. He has had a highly distinguished career that spans appointments with the University of Minnesota where he originally taught and conducted research, the USDA Forest Service where he served as the Regional Silviculturist for Region 5, Oregon State University where he has been a professor since 1981, and most recently a joint appointment with the USGS Forest Rangeland Ecosystem Science Center, where he leads their silviculture and forest ecology research program.

During the course of his career, Dr. Tappeiner has worked in four distinctly different forest regions: the mixed conifer forests of the Sierra Nevada, the red and jack pine forests of the Lake States, the Douglas-fir forests of Oregon and Washington, and the spruce forests of southeast Alaska. He has made important discoveries about the establishment, growth, and development of plant species in all of these regions. Dr. Tappeiner's research is notable because he has taken a broad approach to studying forests. He has examined the effects of silvicultural practices such as thinning and partial cutting on forest structure and composition as well as the ecology of understory species such as vine maple (*Acer circinatum*) and salmon berry (*Rubus spectabilis*). In addition Dr. Tappeiner has had a long-standing interest in understanding how old-growth forests have originated and matured and determining how forests can be managed for the benefit of both wood production and

wildlife habitat. He has published more than 60 refereed journal articles and book chapters and is currently at work on a new silviculture textbook.

Dr. Tappeiner has taken the above findings one step further by showing how the information can be used in an applied fashion. Whether it is promoting browse production of understory shrubs, controlling hardwood sprouts on cutover land, developing thinning regimes in second-growth conifer stands, or accelerating the development of old-growth features, Dr. Tappeiner's work has important implications for silviculturists. Dr. Tappeiner has prepared and delivered countless technical bulletins, agency reports, and conference papers in an effort to disseminate the results of his work and show how it can be used in everyday forestry.

In addition to his direct contributions to science and forestry, Dr. Tappeiner has played an important mentoring role. Virtually all of his research is conducted with colleagues and students, thereby extending the breadth and depth of his efforts. At this point in his career, he has helped train an entire generation of scientists and foresters, many of whom have gone on to noteworthy careers in their own right. His list of co-authors alone is rapidly becoming a "who's who" directory of notable forest ecologists and silviculturists.

In recent years, Dr. Tappeiner has been a thoughtful leader for silviculture in the Pacific Northwest—a region undergoing dramatic change as a result of endangered species listings and other concerns. He was the voice of reason for silvicultural practicality during the FEMAT exercise and subsequent implementation of the President's Northwest Forest Plan. In conjunction with wildlife biologists, forest engineers, and social scientists, he installed an innovative silvicultural trial on the College of Forestry's McDonald-Dunn Research Forest to identify and evaluate alternatives to conventional forestry practices. This study has become a showcase for resource managers interested in pursuing alternative approaches to silviculture that accommodate multiple resource values. He is pioneering similar studies on federal lands in the region.

Dr. Tappeiner's innovations and contributions in the above areas are rooted in his basic scientific curiosity and in openness to new ideas. He also has a knack for viewing old issues in new ways, thereby creating opportunities for alternative approaches to sound silviculture. Such traits rub off on his students and colleagues, further stimulating innovation and discovery.

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Biology, Distribution and Management of Burbot (*Lota lota)* in Washington State

Abstract

There are recent concerns that burbot stocks have been declining in some Northwestern states and Canadian Provinces. Therefore, we investigated the distribution, status and management history of burbot stocks in Washington, and compared their growth, condition, and life history characteristics with those in other regions. Eleven stocks of burbot occurred in eastern Washington, primarily in large, deep lakes and reservoirs of the upper Columbia and Yakima River watersheds. Status of three stocks was known: the Lake Roosevelt burbot stock has increased; the Palmer Lake stock has declined; and the non-indigenous stock in Banks Lake may be extinct. Average growth rate of age 1-10 burbot from four Washington lakes was slower than that in Midwestern states, but similar to that in Alaska, Northern Canada, and Wyoming. Washington burbot over age 10 grew at slower rates than those in all other regions. Average relative weight of Washington burbot was similar to that in reservoirs in other areas of the country, but less than that of lake populations in those other areas. We reported available harvest rates of Washington burbot, but there was insufficient information to determine what impact angler harvest has on most Washington populations.

Introduction

Burbot (*Lota lota*), also known as freshwater ling, is the only freshwater member of the cod family (Gadidae). Burbot are found in fresh and brackish water in northern temperate regions worldwide (Carlander 1969). In North America, burbot are found across the northern United States and Canadian provinces, from Alaska and Labrador south to Oregon, Wyoming, and Connecticut (Wydoski and Whitney 1979). Washington State is near the southern limit of burbot distribution on the west coast of North America, and the species contributes to important recreational fisheries in a few Washington waters.

Recreational burbot catch declined in some British Columbia, Idaho, and Montana waters during the 1980's (McPhail 1997). Burbot declines have been attributed to commercial and recreational overfishing, (Christie 1972, Christie 1974, Parker et al. 1987), hydropower (Paragamian 1995, McPhail 1997), pollution (Christie 1974) and competition with other species of fish (Christie 1974, Carl 1992). We compiled available information on Washington burbot stocks to determine if similar declines had occurred and to gain a better understanding of their status.

Approach

Data on Washington's current and historical burbot distribution and abundance were obtained from: (1) Washington Department of Fish and Wildlife (WDFW) creel, set-line, and gill net surveys conducted statewide between 1965 and 1996; (2) Eastern Washington University and tribal surveys conducted in Lake Roosevelt from 1988 to 1996; (3) historical records from the Washington State Archives and the Washington State Library; and (4) unpublished data and interviews with State, University and Federal fisheries biologists. Depth, size, elevation, and trophic state of Washington

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lakes containing burbot was obtained from Wolcott (1973), Dion et al. (1976) and Sumioka and Dion (1985). The management history of Washington's burbot fisheries was obtained from state fish and wildlife regulations between 1922 to 1995. Additionally, Washington State Archives were consulted for transcripts of State Department of Game Commission meetings addressing burbot issues.

We defined burbot stocks as those groups occurring in individual lakes and reservoirs that were reproductively isolated (Bonar et al. 1997). Origins of stocks (i.e. transplanted or native) were determined through interviews with Federal, State, Local and Tribal biologists, and compilations of historical data from the WDFW and state archives. Status of individual burbot stocks was rated using a four category system developed for Washington salmon stocks (Washington Department of Fisheries et al. 1993, Washington Department of Fish and Wildlife 1997, Bonar et al. 1997). These categories were: (1) healthy—those characterized by increasing or stable long- or short-term abundance, stable condition and stable growth over a 5-10 year period; (2) depressed—those exhibiting a declining trend of abundance, average size or any other factors related to fitness, but declines were above the level where permanent damage to the stock was likely; (3) critical—those experiencing production levels that were so low that permanent damage to the stock was likely or had already occurred; and (4) unknown—those where less than 5-10 years of abundance information was available to rate status.

Biological data on selected stocks were obtained from WDFW creel and set line surveys conducted between 1981 and 1996. Growth of Washington burbot in Chelan, Palmer, Kachess, and Cle Elum Lakes was determined using whole or sectioned otoliths following DeVries and Frie (1996). Relative weights (W_r, Wege and Anderson 1978) of burbot in each lake were determined by dividing the weights of burbot captured in the lake by the standard weight (W_s) of burbot for that length as established by Fisher et al. (1996). Analysis of variance was used to compare growth and condition among lakes in Washington and other regions.

Current Distribution and Habitat

Washington burbot populations probably originated from dispersion of fish from the southern unglaciated portion of the Columbia River basin following the last (Fraser) glaciation, approximately 17,000-13,000 years B.P. (McPhail and Lindsey 1986). Only northern lakes and reservoirs in Washington are known to currently contain burbot and expansion of this species to more southerly regions may be limited by high water temperatures (McPhail and Lindsey 1986).

Eleven Washington lakes and reservoirs in the northern Columbia River drainage, the upper Yakima River drainage, and the Pend Oreille region are known to contain burbot (Figure 1). No burbot have been documented in western Washington, although they inhabit the Skeena River and Nass River drainages in western British Columbia (McPhail and Carveth 1992).

Although there have been sporadic reports of burbot in other Washington waters, there was not enough information to designate these as stocks. Diamond Lake in Pend Oreille County may have contained a small burbot stock prior to 1959, but a piscicide (rotenone) was used to eliminate all fish. One burbot was recovered in 1987 following a subsequent treatment. Isolated "sightings" of burbot were made in canals and seep lakes of the Columbia Basin soon after the irrigation systems were constructed in the 1950's (M. Spence, WDFW unpublished data). To our knowledge, there have been no recent reports of burbot in these systems. Four burbot were captured in Wells and Rocky Reach Reservoirs in 1993. These fish may have been migrants from other areas or came from distinct populations within these systems (Burley and Poe 1994).

Lakes and reservoirs currently containing burbot in Washington are large, ranging from 291 to 31,995 ha, and deep (8 of 11 are over 30 m; Table 1). Of the eight lakes and reservoirs containing burbot where trophic status was measured, five were oligotrophic. They are located at a wide range of elevations, from 280 m to 877 m above sea level, but most tend to be at elevations greater than 600 m.

The habitat burbot use within lakes and reservoirs in Washington is similar to that used in other areas. Burbot tend to inhabit deep water in the southern parts of their range (Robins and Deubler 1955), especially in summer. In our study, burbot were captured at depths of 31-52 m in Lakes Cle Elum, Kachess and Keechelus using set lines; at depths of 25-31 m in Sullivan Lake by jig anglers;

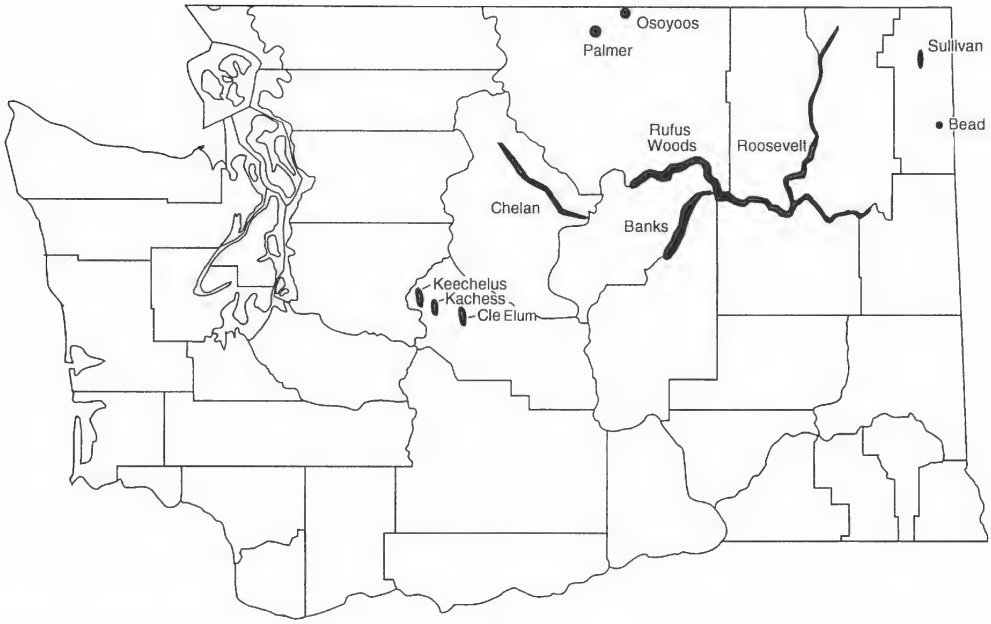

Figure 1. Locations of Washington lakes containing burbot.

TABLE 1. Stock origin, elevation, maximum depth, size and secchi depth trophic state index (TSI) of lakes in Washington where burbot have been captured. Generally, a TSI of >50 is eutrophic, from 40-50 is mesotrophic and <40 is oligotrophic. Trophic state index data was obtained from Sumioka and Dion (1985) and Dion et al. (1976).

Lake	County	Stock Origin	Elevation (m above msl)	Max Depth (m)	Size (ha)	TSI
Banks	Grant	non-indigenous	480	26	10,085	50
Bead	Pend Oreille	indigenous	877	52	291	-
Chelan	Chelan	indigenous	342	494	13,486	28
Cle Elum	Kittitas	indigenous	684	43+	1,948	29
Roosevelt	Stevens, Ferry, Lincoln, Okanogan, & Grant	indigenous	396	115	31,995	-
Kachess	Kittitas	indigenous	694	18+	1839	25
Keechelus	Kittitas	indigenous	774	28+	1037	29
Osoyoos	Okanogan	indigenous	280	63	2,320	45
Palmer	Okanogan	indigenous	352	28	836	47
Rufus Woods	Douglas & Okanogan	unknown	291	58	3,159	-
Sullivan	Pend Oreille	non-indigenous	795	96	559	37

and at depths up to 61 m in Lakes Chelan, Cle Elum, Kachess, Keechelus and Sullivan using gill nets. During winter, burbot often move into shallow water (Bergersen et al. 1993). An intense recreational fishery for burbot occurred in shallow lagoons of Banks Lake during winter in the 1950s and 1960s when burbot were captured through the ice.

Life History

Reproduction

Burbot can either spawn in lakes (Hewson 1955, Robbins and Deubler 1955, Becker 1983, Carl 1992) or rivers (Robins and Deubler 1955, Breeser et al. 1988). In Washington, burbot evidently spawn in lakes and reservoirs except for some Lake

Roosevelt fish that spawn in a flowing section of the Columbia River near the Canadian border (A. Scholtz, Eastern Washington University unpublished data).

Burbot mature at the same rate or more slowly in Washington compared to other regions, depending on the stock. Burbot matured in Lake Cle Elum at 2-4 years (28-43 cm TL). In Palmer Lake, all mature males were six years or older and mature females seven years or older (54 and 64 cm TL, respectively; K. Williams, WDFW unpublished data). Most burbot matured at 3-4 years of age in three Wyoming lakes (Miller 1970), and two years in Lake Winnipeg (Hewson 1955).

Burbot spawn in the winter or early spring in most areas (Cahn 1936, Hewson 1955, Robins and Deubler 1955, Miller 1970, Scott and Crossman 1973), including Washington. Burbot in spawning condition were collected from the Columbia River between mid-February and mid-March (A. Scholtz, Eastern Washington University unpublished data). During the 1950's and the 1960's, the Banks Lake fishery was at its height in late winter in shallow lagoons where burbot were aggregating, reportedly to spawn (M. Spence, WDFW unpublished data). However, two ripe females and one ripe male were captured in WDFW gill net surveys of Lake Chelan during late June, considerably later in the season than usually recorded.

Feeding Habits, Growth, and Condition

Little information is available on growth, condition, and feeding habits of young-of-year burbot of Washington. Burbot fry hatch from early to late spring in other areas (Carl 1992, Ryder and Pesendorfer 1992, Ghan and Sprules 1993). The diet of young-of-year burbot includes amphipods, copepods, and cladocerans (Ryder and Pesendorfer 1992, Ghan and Sprules 1993). Growth during the first five months averaged 16 mm per month in Shebandowan Lake, Ontario (Ryder and Pesendorfer 1992) and burbot grew from 3.2 to 15.0 mm over a 41-day period in Oneida Lake, New York (Ghan and Sprules 1993).

Diet of adult burbot in Washington is similar to that in other areas, where fish can be an important component (Clemens 1951, Hewson 1955, Lawler 1963, Wagner 1972). In Lake Roosevelt, adult burbot preyed on stocked kokanee (*Oncorhynchus nerka,* A. Scholtz, Eastern Washington University unpublished data). Walleye (*Stizostedion vitreum vitreum*), tethered on lines during a hooking mortality study, were also preyed upon heavily by burbot (Bruesewitz et al. 1996). Stomach contents of burbot collected from other Washington lakes have included peamouth (*Mylocheilus caurinus)*, smallmouth bass (*Micropterus dolomieui*), kokanee, rainbow trout (*Oncorhynchus mykiss*, K. Williams, WDFW unpublished data) and Mysids (*Mysis relicta,* Brown 1984; P. Mongillo, WDFW unpublished data).

Average growth of burbot has been estimated for only four Washington lakes. Because of this low sample size, statistical tests used to compare growth in Washington with that in other regions were not powerful enough ($1 - \beta < 0.40$ for all ages) to be meaningful. However, average growth rate of Washington burbot less than 10 years old appears slower than that in the Midwestern states and Canadian provinces, but similar to that in Alaska, northern Canada, and Wyoming (Figure 2). Washington burbot over age 10 also grew at slower rates than those in all other regions. Within Washington, Palmer Lake burbot grew most rapidly, followed by those in Cle Elum and Kachess lakes that had similar growth rates ($P < 0.05$ for lengths at ages 3-9). Growth rates of Lake Chelan burbot appeared similar to those in Cle Elum and Kachess, but this could not be tested since only

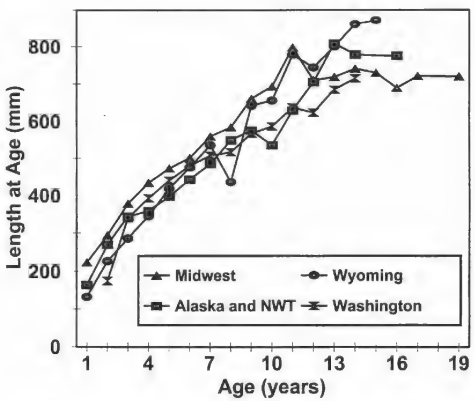

Figure 2. Comparison of mean length at age of lacustrine burbot collected from Midwestern North America (Lawler 1963; Carlander 1969; Bruesewitz 1990) Alaska and the Northwest Territories (Carlander 1969; Parker et al. 1987), Wyoming (Miller 1970), and Washington state.

mean length at age was available for this lake (Figure 3).

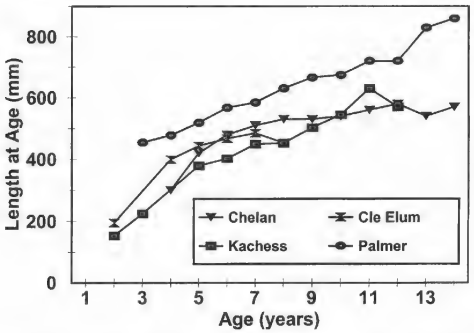

Figure 3. Mean length at age of burbot from four Washington lakes.

Average relative weights for burbot (Fisher et al. 1996) ranged from 43-93 in Washington, with most values in the 80's. These are lower than those usually recorded in large and small North American lakes (approximately 100) but similar to North American riverine and reservoir populations (approximately 80) (Fisher et al. 1996).

The oldest burbot recorded from Washington to date, 19 yr. (741 mm TL), was captured in a gill net in Keechelus Lake. Forty percent of the few fish sampled from this lake were over 10 years old (P. Mongillo, WDFW unpublished data). Burbot over 10 yr. old have been common in catches from other Washington waters. The current state record burbot was caught in January 15, 1993 from Palmer Lake. At a weight of 7.72 kg, its size was impressive, but smaller than some fish reportedly caught from the same lake decades earlier (Meigs 1940).

Status of Individual Stocks

Eight Washington burbot stocks are considered indigenous, two were introduced and the origin of one is unknown (Bonar et al. 1997, Table 1). Of these stocks, we rated one critical (Banks), one depressed (Palmer), one healthy (Roosevelt), and the rest unknown.

Banks Lake, originally known as the "Equalizing Reservoir", appeared to be the only Washington lake where a burbot stock has collapsed. The cause of this collapse was unknown. However this stock was not considered indigenous because the fish likely colonized the lake in the 1950's from Lake Roosevelt. Banks Lake, a 10,085 ha reservoir, was constructed from dams at the north and south ends of Grand Coulee. Water was first pumped into Banks Lake from Lake Roosevelt in the spring of 1951 inundating several small lakes that were already present. Burbot appeared soon after in both the reservoir and adjacent canals (M. Spence, WDFW unpublished data), and fisheries soon followed. In 1965, total burbot catch in Banks Lake was estimated to be 3,250 fish (Spence 1965, cited in Duff 1972). However, the number of burbot in the fishery catch declined 91.6% by 1971-72 to 273 fish (Duff 1972). By the late 1970's, no burbot were reported from the lake. Various explanations have been given for this decline including overfishing; reductions in prey abundance, competition with introduced walleye, and changes in water quality (Bonar et al. 1997). In May, 1988, 192 burbot, averaging 0.6 kg/fish, were transported from Red Rock Reservoir in Montana and stocked into the lake. However, no burbot have been reported in angler catches as of 1999.

The abundance of burbot in Palmer Lake also declined. Angler catch per effort of burbot in the lake was 0.847 fish per angler hour in 1984 and declined to 0.261 fish per angler hour by 1995 (K. Williams, WDFW, unpublished data; F. Bender, unpublished data). High angler harvest and an increase in the abundance of competing smallmouth bass have been cited as possible reasons for the decline.

Burbot were thought to have been introduced into Sullivan lake, a 559 ha natural lake in Pend Oreille county. Burbot appeared in the creel between 1992 and 1994, and a substantial fishery developed. In the winter of 1995, anglers frequently captured 0.9 -1.4 kg burbot with occasional 4.5 kg fish at depths of 25-30 m. No data were available to evaluate population trends in the lake.

Burbot populations in Lake Roosevelt have increased (Underwood and Shields 1996, A. Scholtz, Eastern Washington University unpublished data). Electrofishing catch per effort (CPE) of burbot increased from 0.009 fish/min in 1988 to 0.040 fish/min in 1996. Gill netting CPE of burbot increased from 0.003 fish/hr in 1988 to 0.180 fish/hr in 1996.

Other than these lakes and reservoirs, limited information was available to assess the health of burbot populations. The status of most burbot stocks is still unknown.

Factors Affecting Distribution and Abundance

Harvest History and Management

We found no references to burbot in studies of early Washington tribal fisheries (Ruby and Brown 1970, Horr 1974, Boas and Teit 1985, Chance 1986, Hunn 1990). European settlers first reported burbot from lakes that currently contain the species. Evermann (1899) reported that burbot were occasionally captured in Lake Chelan before the turn of the century and attained lengths of 77 cm and weighed 5.4 kg or more. Mr. C. Robinson of Chelan found a large fish floating in the lake of total length 81 cm, and reported it to the U.S. Fish Commission. Evermann (1899) identified this fish as a burbot based on the description, and reported that it was one of the largest known at that time.

R.C. Meigs (1940) of the Washington Department of Game provided an early description of burbot fishing in Palmer Lake. Meigs reported that "natives" fished the lake heavily each winter with set lines. Each line contained several hooks; each baited with 23-25 cm "chubs" or northern pikeminnow (*Ptychocheilus oregonensis*). Meigs stated that two or three burbot a night, each weighing as much as 16 kg, was a common catch.

Before 1969, burbot fishing was unregulated in Washington. In 1969, burbot were classified as a game fish, but there were no catch or size limits on the species until 1998. From 1971 to 1998, one set line with an unlimited number of hooks was allowed for burbot fishing in Lakes Cle Elum, Kachess, Keechelus, and Palmer. Set lines were also permitted in Lake Chelan, where the number of hooks allowed per line alternated between unlimited and 25. Set line catches in Cle Elum, Kachess Keechelus and Chelan have averaged 4.91 fish per set or 0.240 fish per hook (Table 2).

Fishing for burbot using conventional methods, the most popular of which is jigging, is allowed in all Washington lakes. We found no information to compare catch rates of set lines and jig fishing.

Angler surveys and additional anecdotal evidence from management biologists suggests that burbot harvest on many state lakes is low but increasing. Burbot are the least popular game fish in Washington according to 1986 and 1995 angler surveys (Mongillo and Hahn 1988, Washington Department of Fish and Wildlife 1996). Only 0.2% of Washington anglers preferred fishing for burbot to other species in 1986, while none listed the species as most-preferred in 1996. The percentage of anglers fishing for burbot increased slightly from 1.4% of the total in 1986 to 4.1% in 1995.

Excessive harvest has contributed to decline of burbot abundance outside of Washington State. Commercial overfishing, sea lamprey invasions, and degradation of habitat were identified as major factors contributing to the collapse of burbot populations in the Great Lakes earlier in the last century (Christie 1972, Christie 1974, Jude and Leach 1993). McPhail (1997) reported the collapse of several recreational burbot fisheries in British Columbia, and suggested that a combination of factors, including excessive harvest, may have been responsible. In Alaska, regulations have become increasingly restrictive and monitoring programs have been initiated, as sport exploitation of burbot stocks has grown (Evenson 1988, Bernard et

TABLE 2. Set line catch of burbot in Washington lakes.

Lake	Date	Number of Set line Sets	Average Hooks/ Set Line	Fish/ Set line/Set	Fish/ Hook/Set	Source
Chelan	Spring and Summer 1982 and 1996	22	12.91	6.23	0.483	Brown 1984, Foster et al. 1996
Cle Elum	April, 1989	3	30.67	6.67	0.222	L. Brown, WDFW unpublished data
Kachess	Summer 1989, 1995, 1996	8	36.13	4.75	0.131	S. Bonar, L. Brown, M. Divens, WDFW unpublished data
Keechelus	Summer, 1995	3	16.00	2.00	0.125	M. Divens, WDFW unpublished data
Mean		–	–	4.91	0.240	

al. 1993). To reduce the heavy exploitation occurring on lacustrine Alaskan populations, the number of hooks per set line was reduced from unlimited, to five per day, to two per day, to a total closure of set line fisheries. Since very little jig fishing was directed at burbot, this reduced the overall burbot harvest considerably. Most lakes were closed for 5-6 years, and since then, some populations have rebounded (M. Evenson, Alaska Department of Fish and Game, personal communication). The catch limit of burbot in Montana lakes varies from 5 to 10 depending on the region of the state. However, little is known about most Montana burbot populations. Total catch increased in the popular fishery at Canyon Ferry, but it is not known if this was primarily due to increased burbot numbers or angler pressure (R. Spoon, Montana Department of Fish, Wildlife and Parks, personal communication).

In 1998, the WDFW established a five burbot daily limit statewide, and in those waters where set lines are allowed, the number of hooks was restricted to 10 per angler. These regulations were enacted to help protect populations until monitoring programs could be established to determine which populations, if any, are at risk for overharvest.

Interactions With Other Species

The diet of adult burbot is similar to that of other piscivorus fish such as lake trout (*Salvelinus namaycush*) and walleye; many authors have suggested that these species compete for food. Edsall et al. (1993) saw no lake trout on a Lake Michigan reef containing a high density of burbot, even though large numbers of juvenile lake trout were stocked there annually and temperatures on the reef were in the preferred summer temperature range for lake trout. Day (1983) found that burbot numbers increased and growth declined following a decrease in lake trout numbers in Lake Athapapuskow, Manitoba.

Juvenile burbot may compete with planktivorous or insectivorous fish such as yellow perch (*Perca flavescens*), and juvenile walleye (Clemens 1951). Carl (1992) found no relationship between lake trout and burbot abundance in Lake Openongo, Ontario, but stated that competition and predation from lake herring (*Coregonus artedii*) on larval burbot may have controlled burbot numbers more than competition with lake trout.

Burbot prey on many fish species and serve as food for others. Burbot fingerlings were eaten by nocturnally foraging walleye in an Ontario Lake (Ryder and Pesendorfer 1992). Burbot feed heavily on yellow perch (Clemens 1951, Lawler 1963, Miller 1970, Becker 1983), and Becker (1983) has suggested that burbot may provide a useful biological control for stunted populations of this species. The burbot was the principal coldwater predator of stocked salmonids in Maine lakes (Warner 1972).

Washington burbot usually inhabit lakes containing coldwater species such as trout, kokanee, and whitefish (*Coregonus clupeaformis*). Lake trout were stocked, primarily early this century, in many Washington lakes containing burbot; including Bead, Chelan, Cle Elum, Kachess, and Keechelus. In large Washington reservoirs, such as Banks, Rufus Woods, and Roosevelt, burbot occur with a variety of warmwater and coldwater species including kokanee, whitefish, walleye, smallmouth bass, and yellow perch. While almost nothing is known about the interaction between burbot and other fish species in Washington, interactions which have been documented in other areas probably occur in this state (Clemens 1951, Lawler 1963, Miller 1970, Warner 1972, Day 1983, Carl 1992, Ryder and Pesendorfer 1992). Therefore, stocking lake trout, walleye and other exotics into lakes containing native burbot stocks should be discouraged.

Other Factors Affecting Distribution and Abundance of Burbot.

Burbot abundance can increase after rivers are impounded to form reservoirs (McPhail 1997). Increased larval survival and adult foraging opportunities in impoundments relative to flowing waters may be responsible for these increases. Burbot stocks in Lakes Chelan, Cle Elum, Kachess, and Keechelus, where lake levels were raised, and Roosevelt and Rufus Woods, which are reservoirs in the Columbia system, may have increased following impoundment earlier last century. Downstream of dams, burbot abundance can decline. Paragamian (1995) found a significant relationship between winter power production and the spawning migration of burbot in the Kootenai River, Idaho, and suggested peak winter flows may have reduced the ability of this fish to migrate into spawning areas.

Extreme drawdowns during winter and early spring may either reduce the amount of habitat available to burbot for spawning, or expose eggs

and embryos in the substrate following spawning. Burbot generally spawn in shallow bays or backwaters over a sand or gravel bottom (Cahn 1936, Miller 1970, Scott and Crossman 1973, Becker, 1983). Sand and gravel habitat was exposed during an extreme winter drawdown in Bull Lake, Wyoming, and the remaining substrate in the reservoir consisted primarily of fine silt, which is unsuitable for spawning (Bergersen et al. 1993). No larval burbot were caught following this drawdown in either trawls or traps. At least half of the lakes and reservoirs containing burbot in Washington have experienced significant drawdowns. Reservoir elevations were low at some of these sites during winter or spring (Griffith and Scholtz 1990, Cichosz et al. 1997, U.S. Bureau of Reclamation, unpublished data), which may have limited habitat available to spawning or rearing burbot.

Climate change may also directly or indirectly affect burbot populations. McPhail (1997) suggests that increasing water temperatures may be responsible for some of the reductions in burbot populations recorded in southern regions.

Since burbot occupy a high trophic level, they can accumulate enough trace elements to be unfit for human consumption in some waters. Trace element accumulation in burbot can be high if populations are in close proximity to forest industry wastes and paper mills and these trace elements increase in many reservoirs following impoundment (McPhail 1997). Elevated trace elements in Lake Roosevelt have been of concern for many years because of the discharge of lead-zinc smelters and mining operations (Munn and Short 1997). Lowe et al. (1985) collected several fish species close to Grand Coulee Dam that contained high levels of trace elements. However, Munn and Short (1997) found that trace element concentration in walleye tissue samples from Lake Roosevelt did not exceed the current Federal standard designed to protect the health of people who eat small quantities of fish. Little is known about trace element accumulation in Washington burbot, so studies specific to burbot would be helpful for identifying any potential health risks associated with consuming this species.

Management Implications

The scarcity of information on Washington burbot stocks demonstrates the need for standardized monitoring programs that compare size structure, abundance, growth, and condition of individual burbot stocks to regional averages and evaluate trends over time. Standardized sampling and monitoring programs have been used successfully to assess a variety of fish populations (Ney 1993, Willis and Murphy 1996). Studies in other regions have used underwater video systems along transects (Edsall et al. 1993) and hoop-trapping techniques (Bernard et al. 1991, Bernard et al. 1993) to sample burbot stocks. Monitoring trends in burbot abundance, growth and condition, and relating trends to changes in habitat conditions, harvest, or water quality would help evaluate the status of Washington stocks, and identify factors limiting any stocks at risk.

Washington burbot have the potential to be overharvested because of: (1) increasing angler interest; (2) their slow growth; (3) their advanced age at sexual maturity in some lakes; (4) the few sites where they are found in this state; and (5) the high trophic level that they occupy. Until standardized monitoring programs can be established, conservative harvest regulations and management strategies would aid in preserving self-sustaining stocks in Washington.

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Selenium Levels and Productivity in Three Oregon Elk Herds

Abstract

Selenium (Se) is an essential dietary trace mineral and Se deficiency has been linked to decreased productivity in livestock and some species of wildlife. Productivity of elk *(Cervus elaphus)* in some areas of the Coast, Cascade, and Blue Mountains of Oregon is low or declining, yet the Se status of these herds is unknown. We compared liver Se levels and measures of elk productivity for 447 female elk collected from these 3 geographic regions of Oregon during controlled hunts held in December and January 1987-1993. Elk liver Se concentrations ranged 0.002 - 3.519 ppm, with 42 % of the elk liver samples considered deficient by standards determined for cattle (liver Se $\leq$ 0.120 ppm). Liver Se concentrations varied significantly between areas, and between some years within areas ($P \leq 0.01$). However, liver Se concentration was not related to age, body condition or conception dates of females $\geq$ 1 year of age, and mean herd Se concentration was not related to post season calf:cow ratios, ($P \geq 0.05$). Liver Se was not significant in predicting the probability of pregnancy or lactation in females 3-13 years of age ($P \geq 0.05$). Therefore, we conclude that liver Se levels were not related to the elk productivity parameters we measured. However, liver Se may not be the most appropriate measure of an animal's Se status, because it does not represent a measure of the bioactive form of Se. Instead, we recommend measuring levels of Se in blood.

Introduction

Selenium (Se) is a trace mineral considered by animal nutritionists to be an essential dietary element (Haigh and Hudson 1993, Robbins 1993). It occurs naturally in soils and vegetation worldwide, but its availability varies locally based on geologic history, climate, and land use practices. Se concentrations in $\geq$ 50% of the forage plants of Oregon is inadequate for livestock production ($\leq$ 0.1 ppm) (Haigh and Hudson 1993, National Research Council 1984, 1985).

In animals, Se functions primarily as a component of glutathione peroxidase, an enzyme that prevents oxidative damage to cell membranes and the resulting destruction of animal tissues. Se deficiency in livestock generally manifests itself through decreased productivity, causing reproductive problems in females (i.e. delayed conception, abortions, stillbirths, retained placentas, and mastitis) (Imhof, 1985), and decreased sperm production and motility in males (Hansen and Deguchi 1996). Se deficiency in livestock may also affect feeding efficiency and body condition (Imhof 1985), and may be related to general ill thrift or wasting syndrome in red deer (Knox et al. 1987). Se deficiency can cause myocardial dystrophy and/or white muscle disease in calves (Imhof 1985). Neonate calves with white muscle disease may be unable to nurse or follow their mother and are more susceptible to disease and predation.

Se levels considered less than adequate for livestock production have been measured in a number of game species found in the Pacific Northwest (Fielder 1986, Fleuk 1991, Hebert and Cowan 1991, Hein et al. 1994, Jessup 1990, Oliver et al. 1990, Robbins et al. 1985, Samson et al. 1989, Stoszek 1980), but whether these populations exhibited any symptoms of Se deficiency were not reported. Fielder (1986) theorized that Se deficiency may not exist in wildlife populations because animals may have adapted to patterns of local availability over time by developing alternate chemical pathways to compensate for Se deficient diets. However, Se supplementation of black-tailed deer *(O. h. columbianus)* living in a low Se environment in northern California elevated blood Se levels threefold and increased fawn:doe ratios by 51% (Fleuk 1994), demonstrating that low Se was a factor limiting deer productivity in this area.

Productivity of Oregon's elk is low or declining in some areas. Roosevelt elk (*C. e. roosevelti*) of the Coast Range generally bear calves in alternate years, as opposed to Rocky Mountain elk

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(*C. e. nelsoni*) of the Cascade and Blue Mountains which typically bear calves annually (Trainer 1971). Elk from the south-central Cascades and northeast Oregon have both experienced declining calf:cow ratios in recent decades as low as 26 calves per 100 cows (D. Edwards pers. comm.), but the Se status of these herds has not been determined. Therefore, the purpose of our study was to measure liver Se levels in selected herds of Oregon's elk, and to examine the relationship between liver Se levels and factors associated with elk productivity.

Study Areas

We measured liver Se levels in elk from the Dean Creek elk viewing area in the mid-Oregon coast, the upper North Umpqua River basin in the south central Cascades, and the Starkey Experimental Forest and Range (Starkey) in the Blue Mountains of northeast Oregon (Figure 1). All areas were typical of most managed forest lands in Oregon, consisting of coniferous forests in various seral stages, interspersed with open foraging areas of grasslands, meadows, or recent timber harvests.

Elk from the Dean Creek area were non-migratory, year-round residents of coastal, low elevation, Douglas fir *(Pseudotsuga menziesii)* forests. Primary foraging areas were improved, wet meadows, natural marshes, and recent clearcuts. Wet meadows were improved by seeding winter active grasses and legumes, and by annual applications of fertilizer containing sulfur, boron, and

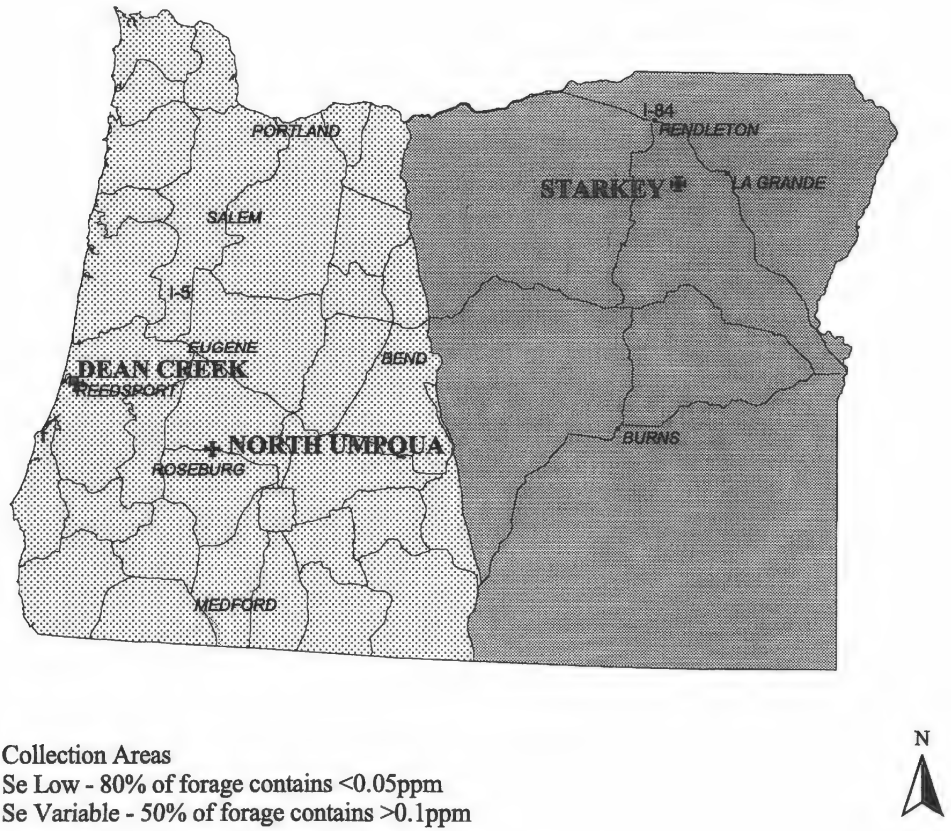

Figure 1. Liver Se collection areas in Oregon. (Reproduced in part from Robbins 1993)

nitrogen. Natural marshes and recent clearcuts contained a mix of coastal, native plant species.

Elk from the North Umpqua area were a mix of resident and migratory elk wintering at higher elevation, mixed coniferous, Douglas fir and white pine *(Pinus monticola)* forests above 915 meters. Primary winter forage areas were small natural meadows, recent clearcuts, and old-growth stands containing a mix of plant species native to the central Cascades. North Umpqua migratory elk summered on four national forests in a variety of habitats and foraged on a diverse array of plant species.

Elk from the Starkey area were confined to a 78-km^2 enclosure of Ponderosa pine *(Pinus ponderosa)* and grand fir *(Abies grandis)* forest. Primary foraging areas were open grasslands of native bluebunch wheatgrass *(Pseudoroegnaria spicata),* and Idaho fescue *(Festuca idahoensis)* and open coniferous stands in various seral stages. Although naturally migratory, Starkey elk were prevented from migrating by a 2.5-m high game-proof fence, baited onto a winter feed area, and fed locally grown alfalfa. A detailed description of Starkey is provided in Noyes et al. 1996 and Rowland et al. 1997.

Methods

Liver sections and reproductive data from female elk $\geq$ 1 year of age were collected in controlled hunts administered by Oregon Department of Fish and Wildlife in December and January 1987-1993. Successful hunters were required to submit samples from harvested female elk, including a liver section, incisor tooth, kidneys with attached fat, udder, and reproductive tract. Liver sections were analyzed by the A.M. Craig Laboratory in the College of Veterinary Medicine, Oregon State University, Corvallis, Oregon for selenium concentrations (ppm) on a wet weight basis using the fluorometric method (Whetter and Ullrey 1978). Age in years, body condition (i.e. kidney fat index, KFI), pregnancy and lactation status, and estimated conception dates were determined as described by Trainer (1971). Annual post-season calf:cow ratios were estimated from helicopter surveys during January and February for Starkey (n = 228 - 434) and North Umpqua (n = 364 - 737) , but herd composition counts from Dean Creek included too few animals (n = 54 - 88) to provide reliable calf:cow ratio estimates.

We obtained data from 145 elk harvested at Dean Creek in 1990 and 1991, 124 elk harvested at North Umpqua in 1987 and 1989-1991, and 178 elk harvested at Starkey in 1989-1993. We used a log10 transformation of Se concentration and a reciprocal transformation of conception dates to improve normality of these variables. Samples for individual elk were pooled by area and year, and these groups of animals were compared using a 1-way ANOVA (BMDP Statistical Software 1991). We used the Fisher's LSD method of multiple comparisons (BMDP Statistical Software 1991) to identify which groups differed significantly. For each group, we used simple linear regression (BMDP Statistical Software 1991) to examine the relationships between liver Se and age, body condition, and estimated conception date of individual elk. We also regressed mean herd liver Se concentration (i.e. mean herd Se) and post-season calf ratios for the year following that in which the Se samples were collected. To determine whether liver Se was a significant variable in predicting the probability of pregnancy or lactation in female elk 3-13 years of age, we used logistic regression (BMDP Statistical Software 1991). In the pregnancy model, we used group, age, KFI, lactation status, and Se as covariates, and for the lactation model, we used group, age, KFI, pregnancy status, and Se as covariates. For all statistical tests we used P = 0.05 as our level of significance.

Results

Elk liver Se levels ranged from 0.002 to 3.519 ppm for all elk sampled (n = 447). Mean liver Se of female elk $\geq$ 1 year of age (i.e. mean herd Se) differed significantly between groups (F = 56.47, 446, 10df, P = 0.00) (Table 1), and was highest in elk from North Umpqua and lowest in elk from Starkey in all years in which data were collected simultaneously on any of the 3 areas. Within each area, mean herd Se varied by year, however the annual patterns of variation were not consistent between areas.

Elk age ranged from 1 to 23 years, but we found no relationship between liver Se concentrations and elk age in any group tested (n = 26 - 64, $r^2 \leq 0.02$, $P \geq 0.23$). Kidney fat indices of body condition ranged from 5 to 415, but KFI's were not related to liver Se in any group tested (n = 16 - 25, $r^2 \leq 0.08$, $P \geq 0.06$). Estimated conception

TABLE 1. Mean liver selenium levels in female elk ≥ 1 year of age (ppm).

Area	Year	N	Mean (SE)[1]	Range
Starkey	1989	36	0.107 (0.009)a	0.015 - 0.293
	1990	30	0.065 (0.008)d	0.002 - 0.160
	1991	41	0.101 (0.049)a	0.050 - 0.186
	1992	34	0.079 (0.007)a	0.018 - 0.195
	1993	37	0.144 (0.006)b	0.072 - 0.313
Dean Creek	1990	71	0.291 (0.032)c	0.032 - 1.266
	1991	74	0.181 (0.024)b	0.039 - 1.558
North Umpqua	1987	28	1.777 (0.196)e	0.117 - 3.519
	1989	27	0.944 (0.154)f	0.073 - 3.026
	1990	43	0.510 (0.068)g	0.055 - 2.172
	1991	26	0.253 (0.037)b,c	0.081 - 0.738

[1] like letters indicate similar means ($P \geq 0.05$)

dates ranged from September 7 to November 24, but we found no relationship between estimated conception dates and liver Se in any group tested ($n = 7 - 37$, $r^2 \leq 0.03$, $P \geq 0.19$). Annual post-season calf:cow ratios ranged from 24 to 57 calves per 100 cows , but calf:cow ratios were not related to mean herd Se ($n = 9$, $r^2 = 0.17$, $P = 0.27$). Liver Se was not a significant predictor of pregnancy ($n = 15 - 46$, $P \geq 0.24$) or lactation status ($n = 15 - 46$, $P \geq 0.07$) in any group test.

Discussion

The wide range of liver Se levels observed in Oregon's elk represents a range considered deficient (≤ 0.120 ppm) to toxic (≥ 1.250 ppm) for cattle (K. Walker, pers. comm.). Livestock in the extreme ends of the range we observed in Oregon's elk would be seriously ill or dead (Imhof, 1985). Twenty-five percent of the elk from North Umpqua had liver Se levels considered toxic for cattle. Although our data were not appropriate for identifying symptoms of Se poisoning (i.e. hoof lesions, stunted growth, skeletal deformities, blindness, and paralysis) (Robbins 1993), none of these symptoms have been reported in elk sampled by hunters.

Fourteen percent of North Umpqua elk, 39% of Dean Creek elk, and 66% of Starkey elk had liver Se levels considered deficient for cattle. Although liver Se varied by area and year, we found no significant relationships between liver Se and any of the productivity parameters we examined and we conclude that they are unrelated. Sample sizes were small and variation between individuals was high resulting in decreased power of some of our tests. However, our findings of significant differences in mean herd Se between areas and years is comparable to other surveys of elk Se levels in the Northwest (Hein et al. 1994, Jessup 1990). Our individual-based analysis of elk liver Se levels and the paired productivity parameters covers a wide range of values, and our consistent lack of any significant relationship further strengthens our conclusion. However, we cannot conclude from our analysis whether Se deficiency does or does not exist in Oregon's elk, nor make recommendations as to the levels at which liver Se becomes deficient or toxic in elk. Only through controlled studies can this be determined. Furthermore, liver samples may not provide the best estimate of Se status in elk. Liver Se concentrations calculated on a wet weight basis may not be as reliable as those calculated on a dry weight basis because of variations in liver water content (D. Hamar pers. comm.) Liver Se concentration does not represent a bioactive level of Se, but rather a stored or reserve amount, and Se stored in the liver may not be available for glutathione production which occurs in the blood only when adequate amounts of vitamin E are present (C. Robbins, pers. comm.). Both high and low liver Se levels can be associated with low blood Se levels, and liver Se levels may appear adequate when blood Se levels are not (C. Robbins pers. comm.). High dietary sulfur and/or heavy metals may also interfere with Se absorption and metabolism (Finch and Turner 1996, Oliver et al.1990), but measures of these chemicals were not obtained or held constant in our study involving free-ranging animals.

Management Implications

We believe that critical levels of liver Se affecting livestock production cannot be applied to elk. However, the significance of adequate dietary Se in optimizing livestock production, and the concerns over declining elk productivity in the Pacific Northwest, suggest a need to better understand the potential effects of Se on elk productivity. In future evaluations of Se status in elk, measures of blood Se levels and concurrent measures of vitamin E and glutathione peroxidase are needed to determine whether Se or vitamin E levels are affecting the production of glutathione peroxidase. Concentrations of sulfur and heavy metals in the

blood would also be useful in evaluating potential inhibitory effects of these chemicals on Se absorption when availability of dietary Se may be otherwise adequate. We recognize that obtaining an adequate number of blood samples from free-ranging elk is logistically difficult in the typical wildlife management context . Therefore, determining whether Se induced productivity problems exist in elk should be determined through highly controlled studies.

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Vertical Stratification of Bat Activity in an Old-Growth Forest in Western Washington

Abstract

We examined the amount and temporal patterns of bat activity at four different heights in an old-growth conifer forest at the Wind River Canopy Crane Research Facility in south-central Washington. Analysis of 2,304 bat passes showed that amount of activity differed among vertical strata. For *Myotis* bats, activity was greatest in the lower canopy, followed by the ground-level and upper canopy, respectively. We did not detect activity of *Myotis* above the canopy. Non-*Myotis* bats used lower and upper canopies more frequently than ground-level and above the canopy. Temporal patterns of activity generally exhibited a bimodal distribution, but the extent of bimodality and the time and relative size of peaks differed with species group and among heights. Activity was greatest at ground-level early in the night and later shifted to higher strata. Patterns of use of old-growth forests by bats may reflect the complex vertical structure of the vegetation in those forests. Exclusive use of ground-based equipment can result in an incomplete picture of the activity of bats in complex forest stands.

Introduction

The vertical and horizontal spatial patterns of trees and other vegetation in forests (forest structure; Oliver and Larson 1996) influence patterns of bat activity. In the Pacific Northwest, Thomas (1988) found old-growth forests supported higher levels of bat activity than did young stands, and hypothesized that differences in levels of activity resulted from increased availability of roosts (large diameter snags) in older forests. Humes et al. (1999) reported similar results, and also found that levels of activity differed among young forests in relation to tree density; amount of bat activity in young stands with low densities of trees was intermediate between young dense stands and old-growth forests. Erikson (1998) found that amount of bat activity differed among age-classes of young managed forests. Hayes and Adam (1996) reported that activity of bats in riparian areas in the Oregon Coast Range was influenced by vegetation, with dramatically lower levels of activity of myotis bats (*Myotis* sp.) in areas that had been clearcut and more activity of larger bats (primarily silver-haired bats, *Lasionycteris noctivagans*) in logged areas. Similarly, in other regions, activity of bats has been shown to be influenced by forest structure (e.g., Fenton et al. 1992, Grindal and Brigham 1998, Kalcounis et al. 1999, Kavanagh and Bamkin 1995, Krusic et al. 1996, Zubaid 1993).

In addition to the influences of forest structure on activity of bats among forest stands, forest structure may also influence patterns of use within forest stands. Because bats use space three-dimensionally, forest structure may influence vertical patterns of bat activity as well as horizontal patterns of use. Kalcounis et al. (1999) examined vertical patterns of use of bats in aspen (*Populus tremuloides*), black spruce (*Picea mariana*), and jack-pine (*Pinus banksiana*) forests in the boreal forest of central Saskatchewan. In aspen forests, they found that *Myotis* were most active within and above the canopy of aspen stands and that there was more activity of hoary bats (*Lasiurus cinereus*) above than below the canopy. However, activity did not significantly differ among heights in spruce or jack-pine forests. Vertical patterns of bat activity in coniferous forests of the Pacific Northwest have not previously been reported.

We examined amounts and patterns of activity of bats in different vertical strata of an old-growth coniferous forest in western Washington. Because old-growth forests in the region are structurally complex (Franklin and Spies 1991), we hypothesized that use by bats would differ among vertical strata. In addition, we hypothesized that patterns of activity would differ among species.

Methods

This study was conducted at the Wind River Canopy Crane Facility, located in the Thornton T. Munger Research Natural Area and the Wind River Experimental Forest in the Gifford Pinchot National Forest. The site is in the southern Wash-

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ington Cascade Mountains, near Carson, Washington, at an elevation of 355 m. The area receives approximately 250 cm of precipitation per year, mostly occurring as rain falling between October and May. The study site is an old-growth forest with an overstory dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*), with western redcedar (*Thuja plicata*), Pacific silver fir (*Abies amabilis*), grand fir (*A. grandis*), and western white pine (*Pinus monticola*) being less abundant. Overstory trees range from 200 to 400 years old with maximum heights of 65 m. Understory trees include Pacific yew (*Taxus brevifolia*) and Pacific dogwood (*Cornus nuttallii*). The most abundant understory shrubs are vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and California hazelnut (*Corylus cornuta* var. *californica*). The canopy structure of the site has been described as "bottom-heavy," indicating that the majority of the vegetation occurs within the lower one quarter of the height of the stand (Parker 1997). The study area is centered on the Wind River canopy crane, a construction crane measuring 74.5 m in height at the jib. The jib of the crane extends 85 m with a counterweight jib extending 35 m in the opposite direction. Bat species that are likely to use the site include Townsend's big-eared bat (*Corynorhynus townsendii*), big brown bat (*Eptesicus fuscus*), silver-haired bat, hoary bat, California myotis (*Myotis californicus*), long-eared myotis (*M. evotis*), little brown myotis (*M. lucifugus*), fringed myotis (*M. thysanodes*), long-legged myotis (*M. volans*), and Yuma myotis (*M. yumanensis*).

We used Anabat II bat detectors (Titley Electronics, Ballina, NSW, Australia), automated with delay switches, to record echolocation calls of bats onto audio tapes (Hayes and Hounihan 1994). To account for potential differences in sensitivity of detectors (Larson and Hayes in press), we calibrated detectors using a Transonix IX pest repeller (Ryans by Mail, Laguna Hills, CA).

We established echolocation monitoring stations at two points for each of four heights: groundlevel, the lower canopy (17 to 25 m above the ground), the upper canopy (35 to 40 m above the ground), and above the canopy (75 m above the ground). Locations of echolocation monitoring stations above the canopy were constrained by the structure of the canopy crane; stations were positioned at the end of the jib and counterweight jib (85 m and 35 m from the crane's center, respectively). Because the crane was allowed to freely spin, or "weathervane," during the night to prevent damage when an operator was not present, location of stations above the canopy could vary both within and among nights. We used the distances to the ends of the jib and counterweight jib to describe two concentric circles surrounding the base of the crane. We located one monitoring station at randomly generated compass bearings along each circle on the ground, lower canopy, and upper canopy. Stations on the ground were placed under plywood shelters to protect the equipment from rain (Hayes and Hounihan 1994). Stations in the lower and upper canopy were placed in plywood shelters suspended between two trees by rope. Stations could not always be placed precisely at the randomly generated points because of the position of trees but each station was positioned within 10 m of the randomly generated point. Detectors on the ground and in the lower and upper canopy were oriented with microphones facing toward the area with the greatest opening. Those above the canopy were oriented with microphones facing perpendicular to the axis of the crane boom. All detectors were tilted upward at a 30-degree angle.

We conducted our study during nine nights between 8 July and 14 August 1996. Generally two, but at least one station at each height was operational each night. Simultaneous sampling at each height allowed us to account for temporal variability among nights (Hayes 1997).

We downloaded and digitized all calls using the ZCAIM Interface and ANABAT 5 software package (Titley Electronics, Ballina, NSW, Australia). Time and location were recorded in file headers created for each call. We examined each pass and noted the minimum and maximum frequency and the duration of calls. Calls were grouped into three broad categories for analysis: 1) calls identified as having characteristics similar to most species of bats in the genus *Myotis* (typically high frequency, short duration calls) were placed in the *Myotis* group (O'Farrell 1997), 2) calls with characteristics similar to the big brown bat, silver-haired bat, hoary bat, and fringed myotis (all with typically low-frequency, long duration calls) were placed into the non-*Myotis* group, and 3) fragmentary calls that did not yield sufficient

information regarding frequency and duration were classified as undetermined. Further taxonomic refinement was not possible because a high percentage of calls were fragmentary.

We examined differences in log-transformed number of passes by vertical stratum using a two-way ANOVA using SAS PROC GLM. We generated least squares estimates of log-transformed means for number of passes in each vertical stratum and conducted multiple comparisons for number of passes among strata using Fisher's protected LSD. To assess temporal patterns of activity, we partitioned the period between sunset and sunrise into 20 equal-length periods (mean = 27.1 min., range 25.5 to 29.6 min.) to account for differences in length of nights during the study period. We then determined the number of passes occurring in each 5-percentile period (Hayes 1997). We used the Kolmogorov-Smirnov Two-Sample Test (Sokal and Rohlf 1995) to examine differences in temporal patterns of use by bats among vertical strata. P-values for the Kolmogorov-Smirnov Test were taken from tables provided by Rohlf and Sokal (1981).

Results

We recorded 2,304 bat passes. Of these, 1,207 (52.4%) were classified as *Myotis,* 154 (6.7%) as non-*Myotis*, and 943 (40.9%) as undetermined.

Significantly different numbers of passes by *Myotis* were detected at each vertical stratum (Table 1). The greatest number of passes were recorded in the lower canopy, followed by the ground-level and upper canopy, respectively. No calls recorded above the canopy were classified as *Myotis*, although it is possible that some of the calls recorded above the canopy and classified as undetermined may have been produced by *Myotis* bats. The patterns observed for undetermined passes and for total passes were similar to that for *Myotis*, as would be expected given the predominance of use by *Myotis* bats in the study area.

The largest number of passes for non-*Myotis* bats were recorded in the upper canopy, followed by the lower canopy, ground-level, and above the canopy (Table 1). Number of passes of non-*Myotis* bats at the ground-level was not significantly different than number of passes recorded above the canopy, and number of passes recorded in the lower canopy did not differ from that recorded in the upper canopy.

Over all vertical strata combined, activity of *Myotis* exhibited a bimodal distribution with peaks during the fifth and ninetieth percentile of the night. However, temporal pattern of activity for *Myotis* at the ground-level differed significantly from that in the lower ($P < 0.005$) and upper ($P < 0.001$) canopy. There was a strong peak in activity of *Myotis* at the ground-level in the first fifth percentile of the night with a smaller and less pronounced peak during the last 15% of the night (Figure 1); 49.7% of all *Myotis* calls recorded at the ground-level were recorded during the first 5% of the night. In contrast, the largest peak in activity in the lower canopy occurred during the last 25% (roughly 2-1/2 hours) of the night; with 53.4% of all *Myotis* passes recorded in the lower canopy during this period (Figure 1). Relative to the pattern observed at ground-level, the early evening peak in activity in the lower canopy was much smaller and was shifted later by roughly one-half hour (one 5-percent interval). The pattern of activity for *Myotis* in the upper canopy showed a slight bimodal tendency, with somewhat more calls recorded during the latter portion of the night than in the earlier portion of the night. Temporal patterns of activity in the lower and upper canopy were not significantly differ-

TABLE 1. Median number of passes across all nights. Confidence intervals (in parentheses) were calculated for log-transformed numbers and back-transformed for ease of interpretation. Median values for number of passes having the same superscript within a column are not significantly different ($P > 0.05$) from one another. Total passes are the sum of passes categorized as *Myotis*, non-*Myotis*, and undetermined.

	Category of passes		
Vertical stratum	*Myotis*	Non-*Myotis*	Total passes
Above canopy	0	0.6 (0.2-1.2)[a]	0.9 (0.4-1.6)[a]
Upper canopy	8.8 (6.5-11.8)[a]	1.8 (1.1-2.7)[b]	22.6 (16.4-30.9)[b]
Lower canopy	27.1 (19.7-37.1)[b]	1.7 (1.0-2.7)[b]	46.5 (32.6-65.7)[c]
Ground-level	15.0 (10.8-20.7)[c]	0.5 (0.1-1.0)[a]	33.8 (23.7-48.1)[bc]

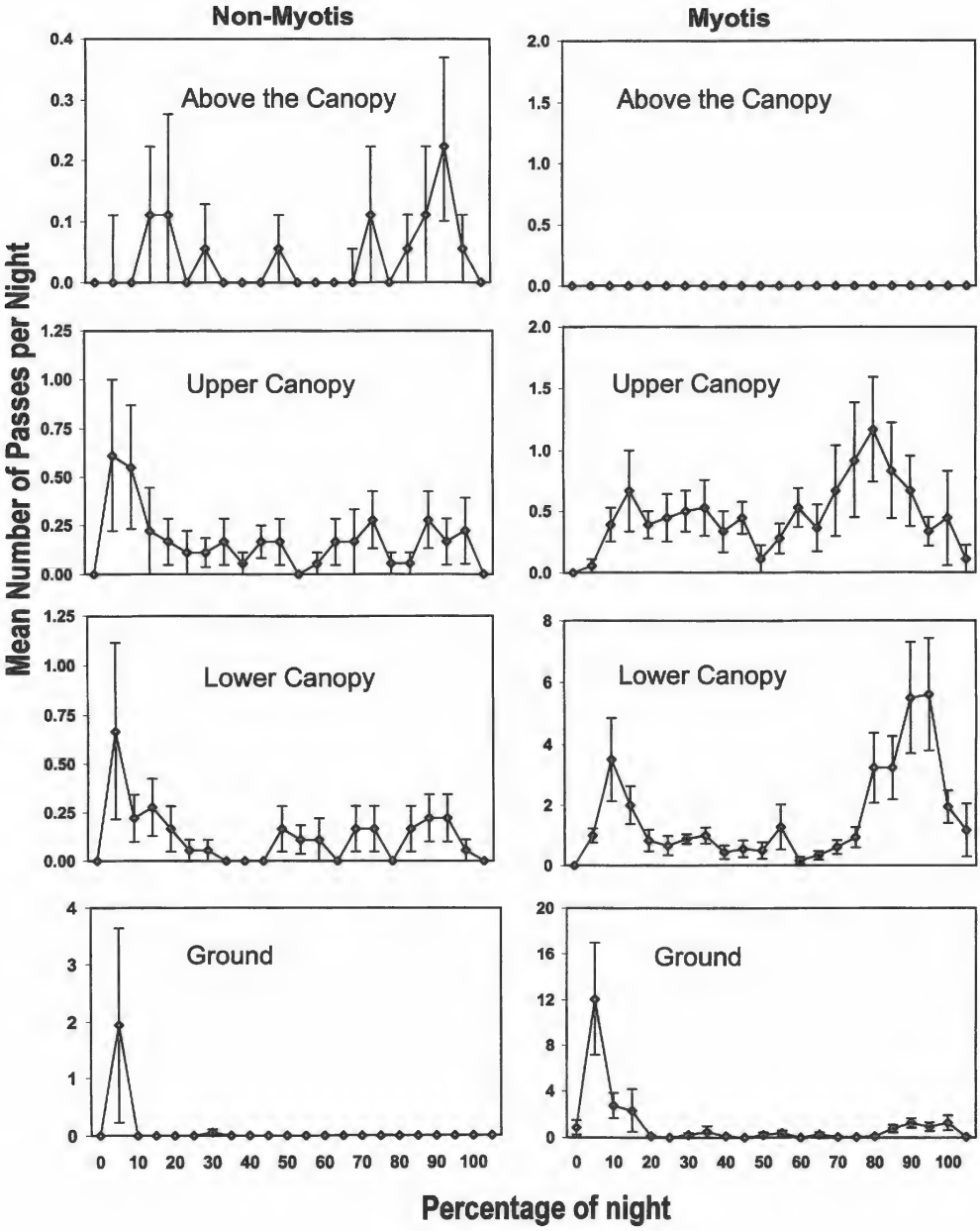

Figure 1. Temporal distribution of activity for passes classified as *Myotis* or as non-*Myotis* for each vertical stratum. Level of activity is scaled differently for each stratum and taxonomic group to illustrate temporal patterns. Passes at 0 and 105% of the night represent all passes recorded prior to sunset and after sunrise, respectively.

ent ($P > 0.10$). Differences in patterns of activity among levels reflect a shift in use of the area over the course of the night. During the initial 5% of the night, over 90% of the *Myotis* passes were recorded at ground-level (Figure 2). Activity then shifted to higher vertical strata with most of the activity occurring in the lower canopy during most of the rest of the night; the predominance of activity in the lower canopy was most pronounced during the last 20% of the night.

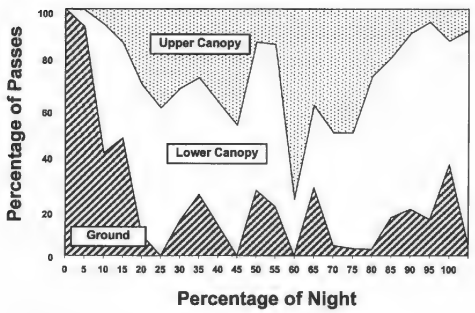

Figure 2. Temporal pattern of relative amount of *Myotis* activity recorded at ground-level, the lower canopy, and the upper canopy. Passes at 0 and 105% of the night represent all passes recorded prior to sunset and after sunrise, respectively.

Non-*Myotis* bats also showed a strong peak in activity during the first 5% of the night, although a second peak later in the night was not evident. The early evening peak was most pronounced at the ground-level (Figure 1); only one pass of non-*Myotis* bats was recorded at ground-level after the first 5% of the night. Less pronounced peaks in non-*Myotis* activity were observed during the first 5% of the night in the lower and upper canopy, and a low, but relatively consistent, amount of activity was recorded throughout the rest of the night. Activity was consistently low throughout the night above the canopy and no distinct modality was evident, although patterns may have been obscured by the extremely small number of calls recorded at that level. The pattern of activity at ground-level for non-*Myotis* bats was significantly different than that observed at each of the other three levels ($P < 0.001$); temporal patterns of activity for non-*Myotis* at the lower canopy, upper canopy, and above the canopy were not significantly different ($P > 0.10$).

Discussion

Studies that monitor echolocation calls to assess activity of bats typically are conducted using bat detectors placed on or very near to the ground. We found patterns of use differed substantially among vertical strata, and that these patterns differed between species groups. Thus, exclusive use of ground-based equipment may result in an incomplete picture of the activity of bats in complex forest stands. Results of echolocation-monitoring studies conducted in forested environments using only ground-based equipment should thus be interpreted with recognition of potential limitations in inference that result from sampling only one vertical stratum (Hayes in press).

The bimodal pattern of activity observed at ground-level for *Myotis* bats is consistent with patterns observed in other studies (Erkert 1982, Hayes 1997, Kunz 1973, Maier 1992, Taylor and O'Neill 1988, Thomas 1988), although the relative magnitude of the peak observed during the early portion of the night in this study exceeds that typically observed. The bimodal pattern of activity of bats in old-growth forests of the Pacific Northwest has been interpreted to result from an initial pulse of activity as bats leave their roost sites, followed by decreased activity in the middle of the night as bats forage in other areas, and a second peak of activity resulting as bats return to their roost sites during early morning hours (Thomas 1988). Others (Hayes 1997, Kunz 1974, Kunz et al. 1975) have attributed the bimodal pattern of activity of bats to an initial period of foraging and roosting after emergence from day roosts, reduced activity in the middle of the night when bats are at night roosts, and a final bout of foraging and commuting before returning to day roosts.

Kalcounis et al. (1999) suggested that vertical shifts in activity may account for temporal patterns of activity observed at ground-level. We observed a shift in activity from ground-level to higher vertical strata through the night (Figure 2), consistent with this hypothesis. The mechanisms responsible for these vertical shifts in activity are not clear, but may be related to vertical shifts in abundance or availability of insects through the night. Shifts in height of activity do not, however, account for all of the observed bimodality in activity, as a bimodal pattern is evident even when all vertical strata are combined. Night-roosting probably accounts for some of this bimodality,

as night-roosting comprises a substantial portion of the activity budget of some species (Anthony et al. 1981, Barclay 1982, Perlmeter 1996) and periods of night-roosting generally overlap with periods when recorded activity is lowest (Adam and Hayes in press, Kunz 1974, Perlmeter 1996). Movement from day-roosts to foraging habitat undoubtedly occurs as well (Waldien 1998), and may account for a portion of the pattern in some habitats.

Myotis and non-*Myotis* bats exhibited different patterns of use of vertical strata. Differences in use of vertical strata between *Myotis* and non-*Myotis* bats in our study may have resulted from a number of factors. Differences in use of habitat among species of bats have been postulated to be related, in part, to differences in abilities to exploit resources with more maneuverable species concentrating use in more cluttered habitats and less maneuverable species predominantly using less cluttered environments (Aldridge and Rautenbach 1987, Brigham et al. 1997, Crome and Richards 1988, Kalcounis and Brigham 1995, Kalcounis et al. 1999, McKenzie and Rolfe 1986, and Norberg and Rayner 1987); this may account for the different patterns of use we observed for *Myotis* and non-*Myotis* species.

The complex vertical structure of old-growth forests in the Pacific Northwest (Franklin and Spies 1991) provides the opportunity for partitioning and exploitation of diverse niches by aerial insectivores, such as bats. Other taxa, including epiphytes (McCune et al. 1997) and birds (Shaw and Flick in press), differ in presence, abundance, or use of habitat at different heights in old-growth coniferous forests. Forests with simple vertical structure, such as young conifer plantations, may not provide a diversity of foraging niches for bats; this may, in part, account for differences in activity of bats in older and younger forests (Thomas 1988, Humes et al. 1999). We were unable to test this hypothesis because our work was limited to a single site, and we could not compare patterns of activity among forests differing in structural complexity. Comparative studies to evaluate this hypothesis through examination of differences in activity of bats at different heights among forests in the Pacific Northwest differing in vertical complexity would be valuable.

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Determinants of the Tailed Frog's Range in British Columbia, Canada

Abstract

The tailed frog is the only stream-breeding frog in Canada. Due to its highly specialized habitat requirements and its vulnerability to habitat degradation, it is of concern through much of its range in the Pacific Northwest. The purpose of this study was to determine the range of the tailed frog in British Columbia, and to generate hypotheses for its current distribution. The tailed frog is a resident of steep mountain streams. Along the coast, other than its absence from Vancouver Island and Haida Gwaii, the tailed frog's distribution coincides closely with the Coastal Western Hemlock (CWH) biogeoclimatic zone. In the interior, an area with a continental climate, its distribution is allied with the Engelmann Spruce/Subalpine Fir (ESSF) biogeoclimatic zone. However, streams in the ESSF are likely only suitable to tadpoles if a thick blanket of snow buffers them from winter freezing. Thus, drier subzones of the ESSF are less likely to support tailed frogs. This close association with moist biogeoclimatic zones may reflect the species preference for a humid temperate climate regime. The tailed frog's distribution may also be associated with geology: in contrast to streams underlain by competent plutonic rocks (e.g., granite), which typically have coarse gravel beds with locked boulder steps, areas with highly fractured or weak rock types (e.g. shale) have a finer and more mobile stream bedload, leading to unstable channel conditions. These streams provide less favorable habitat for tadpoles. Along the coast, the presently documented northern distribution lies at the Nass River, and the factors limiting northward dispersal are not apparent. In the interior of British Columbia, northward advancement appears to be limited in part both to underlying rock type and climate.

Introduction

Aside from a small population of Pacific giant salamander (*Dicamptodon ensatus*) in the extreme southwest of British Columbia, the tailed frog (*Ascaphus truei*) is the only stream-breeding amphibian in Canada (Cook 1984). The tadpole stage may last one to four years during which it is subject to stress or mortality from natural or anthropogenic events that may affect the natal stream channel. Typical mountain streams which support tailed frogs are characterized by a step-pool morphology (see Chin 1989). Step-pool systems have stable bedforms over time spans of 5 years or more, with reorganization occurring during infrequent, extreme events (Chin 1998). This represents long-term stability from the tadpole's point of view. Negative influences include debris flows or flooding (Metter 1964), or increased sedimentation from logging and other land use practices (Corn and Bury 1989; Wahbe 1996; Welsh and Ollivier 1997; Dupuis and Steventon 1999). In Montana, adults appear to recolonize degraded areas relatively slowly (Daugherty and Sheldon 1982). Since it is sensitive to land-use practices, the tailed frog is designated "at risk" in British Columbia, "of concern" in Washington, Oregon, and of special concern in California. Prior to 1990, the Canadian range of the tailed frog was thought to be largely restricted to the southern coast of British Columbia, with some records from the Kitimat/Terrace area on the north coast (Green and Campbell 1984). Based on a 1958 record by J. Grant, confirmed by S. Orchard in 1983, a separate population was assumed to occur in southeastern British Columbia, but its status and extent was unknown.

Because the species is vulnerable to habitat disturbances and is designated "at risk", delineating its current range was important for conservation measures. Based on extensive surveys, we report the range of the tailed frog in British Columbia, and hypothesize on the factors which might affect its current distribution. Although some preliminary tests have been conducted on our database (Sutherland and Bunnell 1999), these hypotheses wait to be explicitly tested.

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Survey Areas

During 1995, 1996 and 1998, field surveys were conducted along 519 creeks in British Columbia. Surveys began at the 49th Parallel and extended to 58° N, a distance of about 1,815 kilometers. Sixty percent of the creeks surveyed were located in the Coast Ranges, from the Sunshine Coast to the Stikine River, in northern British Columbia. Because numerous records were available from the populous, southern coastal portion of the province, extra search effort was focused where historical records were scarce: the mid, northern and eastern portions of the Coast and Mountains Ecoprovince (refer to Demarchi (1993) for an overview of the ecoregions of British Columbia). Given the remote nature of the mainland coast, surveyors had to fly into active logging camps and use logging road access to systematically search every road-accessible permanent creek in the area. The remainder of the surveys (40%) were carried out in southeastern British Columbia between the Akamina-Kishinena and Moyie Rivers. Road access in the east part of the study area was good so all permanent creeks within a 2,000 km^2 area of the single confirmed record (Storm Creek) were searched to delineate the species' northern and western range boundaries in the East Kootenays. Searches of all permanent creeks were also carried out west of the dry Rocky Mountain Trench, within the southern portion of the McGillivray Ranges (1300 km^2 area) because of its proximity to existing populations in northwestern Montana. Additional creeks were surveyed in the adjacent Southern Columbia Mountains.

Methods

Reconnaissance Surveys

Time-constrained searches (TCS) are the most effective technique for determining the presence or absence of a species in an area because they involve no set-up costs, allow for large areas to be covered, and focus on the most suitable microhabitats (Corn and Bury 1990). Time-constrained searches involve hand-raking gravel, uplifting cobbles, sweeping boulder surfaces and scanning the banks for a specific time limit.

Detailed Searches

Area-constrained searches are ideal for determining species density, because they involve the thorough search of a stream segment (e.g., Dupuis and Steventon, 1999). In this study, tadpole density within a creek was estimated by counting all the individuals encountered during an active search of one 10-m segment of stream.

Stream Characterization

A series of physical parameters, following Bury and Corn (1991), were measured to characterize the habitat of each creek. These parameters included aspect, elevation, stream gradient (%), wet and bank widths (m), water temperature (°C), canopy closure (%), understory cover (%) and substrate composition (%). Substrate was classified visually into four categories: sand (<2 mm), pebbles (2-64 mm), cobbles (64-256 mm), and boulders (>256 mm) in accordance with the Udden-Wentworth size classification (Pettijohn et al. 1972). Regional variables included local climate (Meidinger et al. 1997; Meidinger and Pojar 1991), physiography and bedrock geology (Holland, 1976), and landscape units as defined by ecological and topographical parameters (Demarchi 1993).

Compilation of Existing Observations

The final inventory method involved the collection and compilation of existing records (n = 235) from provincial and federal government agencies, academic groups, consultants, naturalists, and museums. Government agencies in Whitehorse, Yukon Territory (Department of Fisheries and Oceans) and Juneau and Ketchikan, Alaska (Department of Fish and Game, U.S. Fish and Wildlife, Tongass National Park) also contributed information. These observations had been collected by various means, including electroshocking, trapping, active searches and opportunistic sightings.

Results

A total of 398 twenty-minute surveys were conducted for a reconnaissance of the remote coast and the southeastern Kootenay Region. This data is summarized in Table 1, for comparable estimates of relative abundance in British Columbia (given the lack of TCS surveys along the south coast, secondary observations for this region are also included in Table 1 for a frequency of occurrence comparison). In addition, 47 reconnaissance surveys were done in which searching ceased after the first detection (absence was

TABLE 1. Frequency of occurrence and relative abundance (mean and range of TCS) of the tailed frog in various parts of its range in British Columbia

Location	No. Creeks Sampled	Occurrence (%)	Mean No. Tadpoles per 20 minutes (range)
Kootenays	188	9	3 (1 - 16)
North Coast	110	15	10 (1 - 34)
Mid Coast	100	36	10 (1 - 34)
South Coast	93*	54	N/A

* secondary observations with no relative abundance data

assumed after 20 minutes). A total of 74 area-constrained searches were conducted near the northern edge of the tailed frog range (n = 53) and in the southeastern corner of the province (n = 21), where specific questions about density were asked.

Tailed frogs were present in 285 of 733 sites searched. Tadpoles were present in approximately 40% of the permanent creeks sampled in central and southern coastal British Columbia (Table 1). Tadpole numbers ranged from 1 to 34 tadpoles per 20-minute search along the mid-coast (Table 1). Occurrence was less common, and relative densities were lower in the northern and eastern portions of their range.

Coast Mountains

The tailed frog's distribution along British Columbia's coast is mostly continuous through the Coast and Mountains Ecoprovinces as far north as the Nass River Basin, from which the species was absent (Figure 1). The most northerly records were along the northwest shore of Kitsemkalum Lake, on the leeward side of the Coast Mountains. Elsewhere in the coastal portion of its range, the distribution of the tailed frog is largely congruent with the distribution of the Coastal Western Hemlock zone (CWH), and associated biogeoclimatic zones at higher elevations (e.g., Mountain Hemlock, Engelmann Spruce-Subalpine Fir, Alpine Tundra). North of the Nass River, tailed frogs were not detected in the Coastal Western Hemlock zone between Greenville and Stewart, or in the isolated pockets of CWH along the Stikine River. Discussions with Alaskan agencies revealed no evidence of the species (e.g., within federal and state parks, and in streams surveyed for fish by means of electroshocking). Thus, it appears that the present range of the tailed frog lies south of Portland Canal and the Nass River.

The most westerly records were found on islands of the mid- and northern-coast of British Columbia: Princess Royal Island and Gribble Island at the mouth of Douglas Channel, and King Island west of Bella Coola. Tailed frogs were also documented as far west as Namu and Boswell Inlet on the eastern edge of the Hecate Lowlands. The most easterly coast records were found in the Cayoosh Ranges between Pemberton and Lillooet, Spius Creek (northeast of Boston Bar), and Cathedral Park (south of Princeton)(Figure 1). These areas fall just beyond the Coast and Mountains ecoprovince, within the Southern Interior Ecoprovince (Demarchi 1993).

East Kootenays

Tailed frogs occurred in 9% of 188 creeks sampled in the East Kootenays (Table 1), and are limited to a few southern drainages of the Southern Interior Mountains Ecoprovince (Figure 1). In 1996 and 1998, the species was found in ten tributaries that flow into the Flathead Drainage near the Montana border. Tailed frogs were also encountered in six tributaries to Yahk River, in the Columbia Basin. These occurrences coincide with the Border and McGillivray Ranges, respectively, which are separated by the Rocky Mountain Trench. Tadpoles and adults were found at high elevations (1380 to 1770 m), within the Engelmann Spruce/Sub-alpine Fir (ESSF) biogeoclimatic zone (Meidinger and Pojar 1991).

Green and Campbell (1984) and Nussbaum et al. (1983) provide two records further north in eastern British Columbia, near Shuswap Lake. These records are false (Green, pers. com. 1999) and likely propagated amongst general amphibian field guides that made use of the same databases.

Discussion

During the last glaciation (ca. 29,000-10,000 C^{14} years B.P.; Clague 1989), the Cordilleran ice sheet extended just south of the 49th parallel into parts of Washington, Idaho, and Montana. Thus, the present distribution of tailed frog populations in British Columbia represents northward migration from southern refugia. Although coastal refugia existed in British Columbia during glaciation (e.g. Brooks Peninsula and parts of Haida Gwaii), the habitats available in these refugia (e.g., nunataks and coastal plain; see Clague 1989; Josenhans et

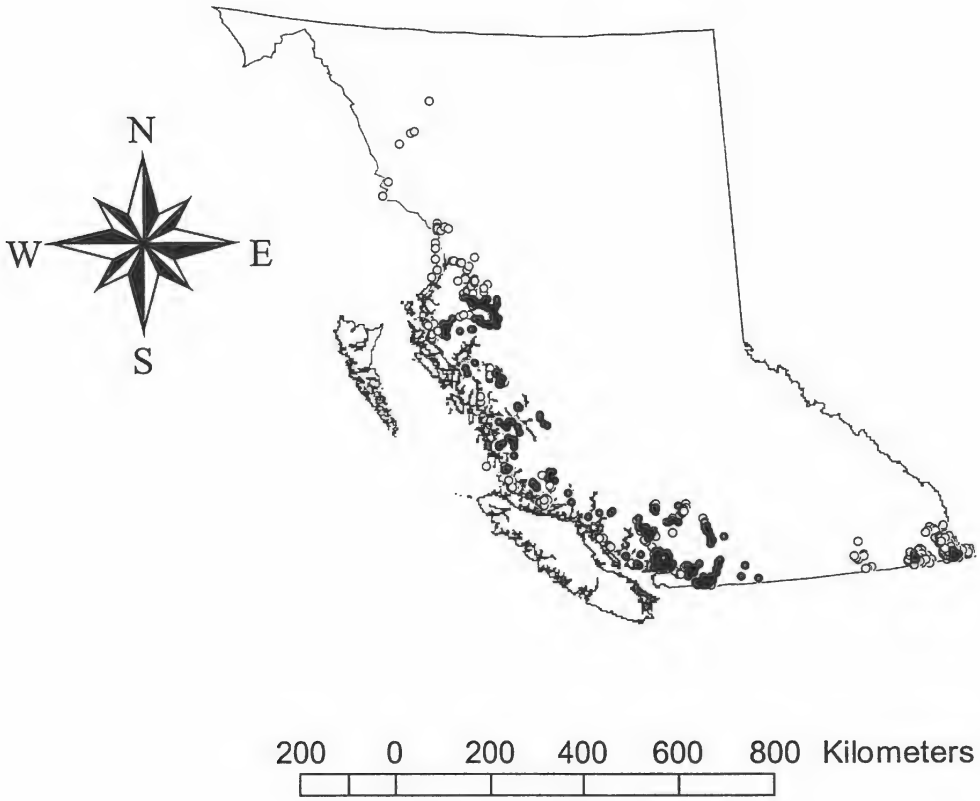

Figure 1. Distribution of the tailed frog in British Columbia; solid dots depict their presence and hollow dots represent searches in which they were undetected.

al. 1997) would not have been suitable to the tailed frog because they lacked permanent, fast-flowing streams in a favorable (temperate) climate. The populations in British Columbia represent northward migration from founding populations in the American Coast Mountains in the west and the Bitterroot and Rocky Mountains in the east. Nowhere in its range is the species found in low relief basins and plateau country, especially if occupied by grassland. Since the climate of the early Holocene (ca. 10, 000 - 7, 000 C^{14} years B.P.) was warm and dry (Mathewes 1985), grasslands of the central interior plateau were more extensive (Hebda 1982), representing a greater barrier than today. Therefore, in British Columbia, coastal and interior populations have probably been geographically isolated for at least 10 000 years. Geographic isolation of coastal and interior populations in the United States has probably been considerably longer.

Other than its apparent absence from Vancouver Island and Haida Gwaii (Corkran and Thoms 1996), the range of the tailed frog in British Columbia coincides closely with the distribution of the Coastal Western Hemlock (CWH) zone and with scattered occurrences in the neighboring zones. This close association is directly related to the species' preferred habitat. The tailed frog breeds in cool, swift flowing headwater streams (Leonard et al. 1993; Corkran and Thoms 1996). Since tadpoles in British Columbia require 3-4 years to develop, suitable streams must be perennial. The CWH zone receives abundant precipitation (Table 2), providing numerous perennial first and second order streams, with enough snow

TABLE 2. Climate regimes associated with tailed frog occurrence.

BGC[1] Zone	Elevation (M)	MAP[2] (mm)	MWP[3] (mm)	MAS[4] (mm)	MAT[5] (°C)	Tailed Frog Occurrence
CWH	0-900	836-4400	695-3313	204-841	4.0-10.7	Throughout
IDF	122-1330	276-1199	117-1022	81-507	1.5-9.6	Wetter portions
MH	400-1800	1700-5000	1200-3000	700-3000	-1.4-5.0	Scattered
ESSF	770-1945	414-2169	170-1607	198-1974	-3.1-3.8	Scattered

[1] BGC = biogeoclimatic zones: Coastal Western Hemlock (CWH), Interior Douglas Fir (IDF), Mountain Hemlock (MH), Interior Cedar Hemlock (ICH), Montane Spruce (MS) and Engelmann Spruce-Subalpine fir (ESSF).
[2] MAP = Mean Annual Precipitation
[3] MWP = Mean Winter Precipitation
[4] MAS = Means Annual Snow (water equivalent)
[5] MAT = Mean Annual Temperature
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cover that many of these streams do not freeze during winter.

Inland from coastal British Columbia, precipitation diminishes and the climate becomes more continental: small streams are fewer and many freeze in the winter. Sampling across the Duffey Lake and Hurley Pass roads, which cross from the coast to the interior, revealed a marked decline in occurrence of tailed frogs at the transition from CWH to ESSF forest. In general, the ESSF zone is cold (Table 2) and shows marked variability in precipitation with most falling as snow (Meidinger and Pojar 1991). Tailed frogs were found at a few sites (n = 9) in the ESSF (near Princeton, Cranbrook, and in Kootenays), suggesting that where the snow blanket is sufficient to permit flowing water, the species can survive in cold climates. The Alpine Tundra zone which lies above the CWH and ESSF was not searched; however, G. Hazelwood (1993) reported adults from alpine meadows above mountain hemlock forests on the windward side of the Coast Mountains. As in the ESSF, distribution in the Mountain Hemlock and Alpine Tundra zones are likely determined by depth of insulating snow cover during winter. The climate regimes associated with tailed frog occurrences are summarized in Table 2.

Although precipitation is essential, extreme rainfall may be detrimental. This notion derives from sampling along a latitudinal transect across the northern Coast Mountains, in the vicinity of Prince Rupert, in a region of similar bedrock geology and local relief. On the windward side, populations were small and scattered (e.g., Scotia River) whereas on the leeward side, they were larger and widespread (e.g., Kitimat River). The change in tadpole densities coincides with a marked shift in precipitation levels, which are twice as high on the windward side of the Coast Mountains (e.g. 4400 versus 2300 mm as measured at valley bottom stations; Meidinger and Pojar 1991). Higher precipitation levels correlate with more frequent and intense rainfall, which may subject tailed frog tadpoles to more frequent and extreme bedload transport events, therefore limiting the viability of tadpole populations in northern coastal watersheds.

Tailed frog distribution is also influenced by geology (Sutherland and Bunnell 1999). Underlying geology influences the character of stream substrates. Massive, competent rock types (e.g., granitic) generally produce coarser substrates that are optimal habitats (Altig and Brodie 1972; Hawkins 1988), while fractured or brittle rock types (e.g., sedimentary) produce abundant fine gravel and sand, which is suboptimal (Dupuis and Steventon 1999; Welsh and Ollivier 1997; Wahbe 1996). Other factors (precipitation, relief) being equal, coarser substrates tend to be more stable and massive bedload transport events are fewer. Coarse substrates also provide greater interstitial habitat and refugia in the face of channel disturbance events. Thus, habitat is better and mortality may be lower in streams underlain by competent rocks.

In British Columbia, competent granitic and metamorphic rocks of the Coast Plutonic Complex underlie the main ranges of the Coast Mountains. Thus, in general the Coast Mountains provide good stream substrate; however, local bedrock structure, such as faults or intense fracturing, may reduce viability of specific streams. East and west of the intrusive spine of the Coast Mountains are older volcanic and sedimentary rocks. These areas provide less suitable substrates. In the East Kootenays, bedrock consists primarily of sedimentary rock, and stream channels are typically underlain by fine gravel composed of angular clasts (rubble). This sediment is readily mobilized and channel substrates are unstable. The Nass Basin, also underlain by fine sedimentary rock (argillitte) is devoid of tailed frogs and may present a barrier to northeastward migration of the species.

In summary, the tailed frog's range in British Columbia appears to be associated with past and current climatic and geological conditions. These geoclimatic factors interplay to produce the patchy distribution of tailed frog populations seen within British Columbia today. In general, the combination of mountainous terrain, plutonic rocks, and maritime climate on the coast provides an extensive region with optimal habitat conditions, while interior habitats with continental climate and sedimentary rock types are considered marginal.

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Comparison of Topographic and Physiographic Properties Measured on the Ground with Those Derived from Digital Elevation Models

Abstract

With the widespread availability of digital elevation models (DEM) and regional surveys of soils, topographic and physiographic features of landscapes are now more easily characterized. Within southwestern Oregon 391 field plots were registered within a geographic information system (GIS) to digitized topographic and soils coverages and properties extracted from the digital coverages compared with those estimated in the field. The initial comparison showed major differences in estimates of aspect, slope, and maximum available soil water content (θ), although the location of plots showed general agreement with elevations recorded on the maps. To extrapolate climatic data and interpret hydrologic responses accurately, an automated search procedure was developed whereby the initial location of each plot was, if necessary, shifted within specified bounds to give closer agreement with field estimates of aspect, slope, and θ. Specifically, the search routine sequentially identifies the nearest 100 m-resolution cell within a search radius of 3 or 5 cells in which differences are within ± 22.5° of aspect, ± 20% of slope, and in closest agreement with field estimates of θ. The search procedure resulted in improved agreement with field estimates: r^2s = 0.82 for aspect, 0.56 for slope, 0.54 for θ. To obtain these improvements required that the initial plot locations be shifted, on the average, 289m within the 3-pixel search radius, and 435 m within the 5 pixel radius. With the terrain analysis procedures developed in this paper, it is possible to overcome many problems associated with registering the precise location of field plots upon digitized topographic and soil maps. The procedure is particularly appropriate in situations where the environmental regimes associated with a specified field location are to be extrapolated across landscapes. The approach also permits a wealth of historical survey plot data to be incorporated into a GIS format and to be spatially extended.

Introduction

Basic information on geographic location, elevation, slope and aspect are collected in most soil and vegetation surveys. Additionally, soil properties are often characterized to provide estimates of maximum available soil water storage in mm (θ) and drainage conditions. Indirectly, these topographic and physiographic features affect the growth and distribution of vegetation as well as the hydrologic response of landscapes to precipitation (Running et al. 1989; Running 1994, Waring and Running 1998). Although soil surveys generally provide broad estimates of θ, a number of studies have demonstrated that local spatial variation of topographic features helps to explain much of the variation in soil water capacity (50m to 200 m) (Band 1986; Band et al. 1993; Nemani et al. 1993). Compared to traditional methods of estimating θ from soil series data, estimates derived from digital elevation models (DEM) provide additional information because topographic data are collected at higher resolution than soil series data.

The possibility of spatially classifying estimates of terrain variability within a digital environment has become possible with the development of terrain analysis programs and DEMs. The general trend in representations of terrain for environmental modelling has been to move from broad, continental and regional scales, to finer scales more suited to the modelling of surface hydrology, vegetation and soil properties. This trend can be attributed to improvements in methods for representing fine scale topographic shape and structure, supported by the steady increase in the speed and storage capacity of computing platforms.

Fine scale DEMs, with spatial resolutions from 5 to 100 m, are typically used for spatially distributed hydrological modelling (Binley and Beven 1992, Zhang and Montgomery 1994) and for the analysis of soil properties (Gessler et al. 1996). The determination of appropriate spatial scales for hydrological modelling is an active research issue (Bloschl and Sivaplan 1995). Terrain attributes can be referred to as DEM derivatives as their calculation is based upon first-order and second-order derivatives of a continuous 3-D surface. The surface can be based on a combination of discrete tiles, grids, or triangular regular networks (TINs), or contour segments. In any case, the algorithms are approximations of those for continuous surfaces. Moore et al. (1991) reviewed the applications of digital terrain modeling and

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listed the major primary terrain attributes that could be derived from a DEM and their application.

Grid based DEMs are developed directly from standard digital topographic data which may include spot heights, elevation contours, stream lines and dams and lakes. The method produces DEMs which respect surface shape and drainage. It can use stream line data, without associated elevation data, to aid the representation of surface drainage. The ready availability of DEMs does not imply however, that they are without error and often are not always available at the most appropriate scale (Hutchinson 1999). In addition, there are a number of potential errors associated with DEMs that are independent of scale:

(a) coastal and flat areas may be represented as terraces due to slope calculations made where flat areas alternate with narrow bands of steeper slopes.

(b) interpolation errors may result over surfaces caused by methods failing to interpret contour data correctly.

(c) local peaks not modeled at their correct height and will appear to be flattened due to poor placement of base spot height data.

(d) offsets related to slope direction and steepness on one side of a topographic feature will result in an overestimate of elevation on one side and an underestimate on the other.

Linking historical data collected at specific points within the DEM requires adjusting for errors that may occur in assigning the initial location of plots to maps that differ in accuracy from those now available and were located without global positioning satellite (GPS) technology. Fortunately, it is now possible, using automated searching logic to examine the geographic position of each plot location with respect to its local terrain and predict its most likely geographic position on current DEMs.

The objective of this paper is to present a approach which compares plot-based measurements of terrain variables with calculations made from a 100 m-resolution DEM and employs an algorithm that searches, within a defined radius, DEM cells to predict the most likely position of the plot within the landscape. Once located, estimates of slope and aspect are extracted from the DEM and θ is predicted with a generalized model derived from topographic and soil series data.

Study Area and Data

The region of southwest Oregon lying between the southern Cascade Mountains and Pacific Coast is an area of great diversity in climate, geology, and vegetation. The developing patterns in vegetation differ, depending on the topographic location and differences in parent material. At lower elevations near the coast, Port-Orford cedar (*Chamaecyparis lawsoniana* (A. Murr.) Parl.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) are common on moist sites. At higher elevation where a winter snowpack accumulates, Shasta red fir (*Abies magnifica* var. *shastensis* Murr. Lemm.) and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) dominate. At mid-elevations on drier sites, Douglas-fir is often accompanied by tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), western white pine (*Pinus monticola* Dougl. ex D. Don) and sugar pine (*Pinus lambertiana* Dougl.). On the most extreme sites with shallow soils or inhospitable parent materials derived from serpentine or peridotite, ponderosa pine (*Pinus ponderosa* Dougl. ex Loud), canyon live oak (*Quercus chrysolepsis* Liebm.) and Jeffrey pine (*Pinus jeffreyi* (Grev. and Balf.)) are present (Whittaker 1960, Franklin and Dyrness 1973).

Plot Data

From 1981 to 1983 a series of temporary plots were established as a forest growth modeling project within the southwest Oregon Forestry Intensified Research Program (Hann and Ritchie 1988, Hann and Wang 1990, Hann and Larsen 1991). A total of 384 forest stands ranging in size from 2 to 47 ha were selected for field sampling. A total of 391 temporary research plots were established in these stands covering an area of 54,000 km^2. The research plots were placed in a cluster design of 4 to 10 sampling units over 1.5 to 4 ha. A modal soil pit was dug at the sampling unit judged to be the most representative of the cluster based on soil attributes. The aspect and slope were measured and the depth and soil texture described by horizons down to 1.4 m or to bedrock were recorded. The maximum available soil water content (θ) was estimated by accounting for variation in soil texture and rock content down to the maximum defined depth (Hann 1983). The geographic location and elevation of each plot was estimated from U.S.G.S. 15 minute topographic maps. For the remainder of this paper, the slope,

aspect, elevation and geographic position of the sampling unit which contained the soil pit will be used to represent the plot as a whole.

DEM Data

Digital elevation data for southwestern Oregon were obtained from the Defense Mapping Agency (DMA, Portland Oregon) with an initial pixel resolution of 80 m. The data were then rectified to 100-m pixel resolution and registered on the Universal Transverse Mercator map projection. A general description of the DEM properties is presented in Table 1.

TABLE 1. Properties of the Digitized Elevation Model for Southwestern Oregon.

Position	Easting	Northing	Cell size (m)
Top Left	305500	4805000	100
Bottom Right	598000	4640000	100

A number of terrain attributes were calculated from the DEM surface. The first and simplest variable to extract was site elevation. The slope of each pixel was calculated by fitting a plane to the difference in elevation between a central cell and the immediately adjacent 3 X 3 array of 100 m cells. The direction that the plane faced defined the aspect for the central cell following the average maximum technique described by Zeverbergen and Thorne (1987) and Moore et al. (1991). To define the direction of water flow through the central cell, the steepest descent of each cell in the 3 X 3 array was estimated following the methods of Jenson and Domingue (1988). The flow accumulation was calculated on a cell by cell basis to take account of the total up-slope area that drained into and through a selected central cell.

The Compound Topographic Index (CTI) (unitless) was computed as a function of the contributing area up-slope of a central cell and the slope at that central cell (Moore et al. 1991). The CTI is calculated as:

$$CTI = \ln\left(\frac{\alpha}{\tan(\beta)}\right) \quad (1)$$

Where α is the up-slope contributing area and β is the slope.

In areas with negligible slope, a CTI value of 0.001 was assigned. This value is smaller than that obtained from a 100 m data set differing in elevation by 1 m. The CTI was originally used in hydrologic models for small basins with high values indicating a greater likelihood of a saturated contributing area (Kirkby and Weyman 1974, Beven and Kirkby 1979; Beven and Wood 1983). The higher values of CTI tend to be found at the lower parts of watersheds and in convergent hollow areas associated with soils of low hydraulic conductivity or areas with more gentle slope than average (Beven and Wood 1983). Soil depth and silt and clay content tend to increase from ridge tops to the valley bottoms (Singer and Munns 1987). Soil erosion is also related to the direction of water flow, with the rates highly dependent upon the degree that soils remain saturated (Zheng et al. 1996).

Soils Data

There is a wide variety information on soils available at varying spatial scales. Within the United States, the U.S. Department of Agriculture's (USDA) Natural Resources Conservation Service (NRCS), formerly the Soil Conservation Service (SCS), leads the National Cooperative Soil Survey (NCSS) and is responsible for collecting, storing, maintaining, and distributing soil survey information for privately owned lands in the United States.

For regional scale mapping and monitoring the State Soil Geographic (STATSGO) data base is the most appropriate because it has been compiled at a consistent scale for all of the United States (United States Department of Agriculture 1991). STATSGO soil data are compiled from more detailed State Survey Geographic Data Base (SSURGO) soil survey maps and information on geology, topography, climate, and vegetation, supplemented by images derived through remote sensing from satellites. Using the United States Geological Survey's (USGS) 1:250,000 scale, 1-by 2-degree quadrangle series as a map base, the soil data are digitized as line segments to comply with national guidelines and standards. STATSCO soil data are often inadequate for local or even regional modeling, especially in mountainous areas. These inadequacies reflect the variation present within cells, insufficient sampling of each mapping unit, and difficulty of drawing boundaries between two different mapping units (Burrough 1986, Mark and Csillag 1990). Never the less, the STATSCO data base provides the only available

state- wide mapping of soil attributes carried out in a consistent manner.

For each soil series, the thickness of each soil horizon and its mean available soil water capacity was computed and summed for the entire profile to provide an estimate of θ for each polygon. This vector coverage was then converted to raster format with a spatial resolution (size of the cell) of 250 m, approximately equivalent to a 1:250,000 scale. If an individual cell was composed of polygons representing more than one soil series, the spatially dominant series was selected.

Soil Water Model

Although it was possible to develop regressions between field estimates of θ and those interpreted from the STATSCO data set, there are advantages in attempting to predict θ directly from hydrological models. First, regression relationships cannot be used in regions where STATSCO data are not available and second, static models make it difficult to assess the dynamic impact of large storms and the implications of road building and other activities on water movement. Zheng et al. (1996) proposed a simple model to estimate θ using the mean values of θ from the STATSCO data set to transform the fine-scale variation defined with the CTI. Equation 2 shows that a general positive relationship exits between CTI and θ (in mm) such that:

$$\theta = \{M_1, M_2\} \cdot \ln\left(\frac{\alpha}{\tan(\beta)}\right) \quad (2)$$

where M_1 and M_2 are case-specific coefficients, one of which is chosen for each pixel. Zheng *et al.* (1996) showed that the distributions of the calculated CTI when compared to θ as obtained from STATSCO datasets were always smaller with longer tails in the high end. Thus, two scalars are needed to avoid transforming right-skewed distributions of CTI into right-skewed distributions of θ. When a pixel's CTI value is less than or equal to its mean, the coefficient M_1, is used in Equation 2. M_1 is determined in equation 3 by:

$$M = \frac{\theta_{(STATSCO)me}}{0.5 \cdot (CTI_{mo} + CTI_{mean})} \quad (3)$$

where CTI_{mo} and CTI_{mean} are mode and mean values of the calculated CTI, respectively and $\theta_{STATSCO}$ is the mean value θ for a given spatial extent, estimated from either the mean of the STATSCO θ or other relevant data. The function of M_1 is to re-scale the CTI values that are less than or equal to its mean at a rate for which the median value of CTI is equal to $\theta_{STATSCO}$.

When a pixel's CTI value is greater than its mean, the coefficient M_2 is used in Equation 2 and is estimated by equation 4:

$$M_2 = \frac{\theta_{(STATSCO)max}}{CTI_{max})} \quad (4)$$

where $\theta_{(STATSCO)max}$ is the maximum θ occurring in the STATSCO database for the region and CTI_{max} is the maximum CTI value with an occurrence rate at least 1%. Again, θ_{max} can be estimated for a given spatial extent from maximum STATSCO layer or from other relevant data. The function of M_2 is to re-scale CTI values that are larger than the CTI mean at the rate that makes the defined maximum CTI value equal to θ_{max}.

In this study, M_1 for Southwestern Oregon (100-m pixel resolution) was 17.4 / (0.5 * (3.8 + 1.3)) = 6.8. The maximum calculated CTI value with an occurrence rate of over 1% was determined to be 16.3. A value of 40 cm was used for the maximum θ from STATSCO to determine M_2 for Southwestern Oregon. These different maximum values are close to the maximum value of θ estimated from field surveys (Table 2).

TABLE 2. Summary of input data used in the search routine to re-position field plots.

Data set	CTI	STATSCO (θ) (mm)	Plot Data (θ) (mm)
Pixel Resolution (m)	100	250	-
Number Plots	-	-	391
Number Polygons	-	1314	-
Number Pixels	3304394	-	-
Mean	3.8	168	174
Maximum	24	400	269
Minimum	0	0	39
Mode	1.3	51	157

GIS Search Algorithm

An initial test of the accuracy of the initial plot positions and the compatibility of the elevation, slope, and aspect data with the cell-based predictions was completed for all 391 plots. Based on this initial comparison, a search algorithm was developed to interrogate individual pixels within

a specified rectangular subset of cells (known as a boxcar) that exhibit similar slope, aspect, and θ attributes as those recorded in the field.

If each plot was located accurately, and the terrain attributes were all calculated without error, then the central pixel in the boxcar would share all the attributes recorded at the field plot, a situation that rarely happens.

The formal computation presented in the algorithm can be described in equation 5.

$$W(P)_{i,j} = \min_{n=1}^{n=m} P(Aspect, Slope, \theta)_{i,j} - P(Aspect, Slope, \theta) \quad (5)$$

where $W_{i,j}$ is the re-computed geographic position of plot P, P(Aspect, Slope, $\theta)_{i,j}$ are the terrain attributes for the cell coincident with the original plot location on the DEM, and P(Aspect, Slope, θ) is the aspect, slope and θ, as recorded in the field at the plot location. The search is undertaken for all cells from n = 1 to n = m where m is the number of cells.

The operational steps are shown diagrammatically in Figure 1 and are applied for each plot as follows:

- Initially, the plot aspect is compared to the aspect of all cells in a specified boxcar filter. If any cells have aspects that lie within ± 22.5°, the cells are tagged as acceptable candidates.

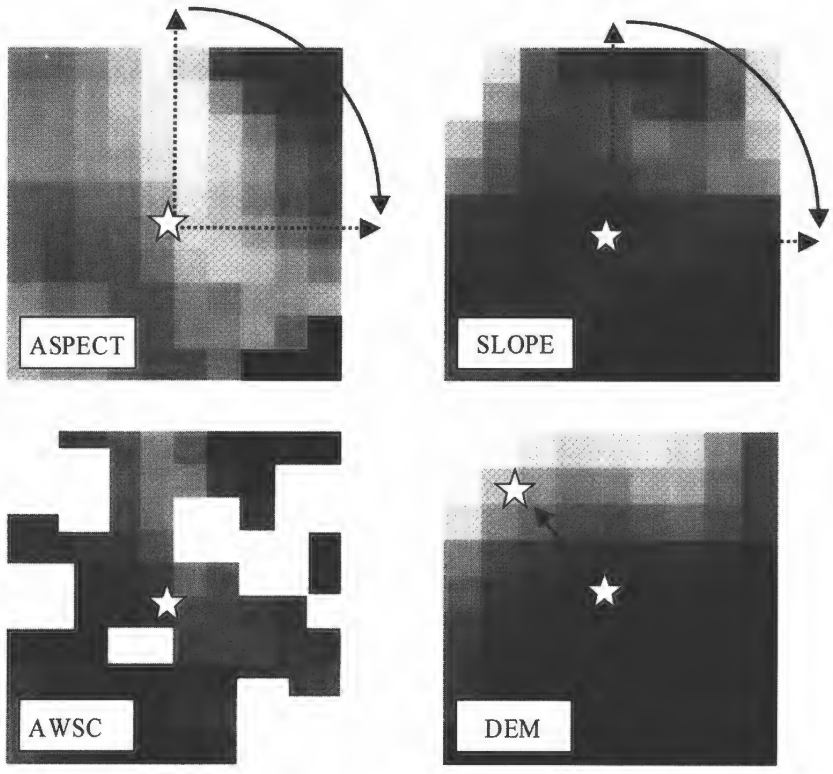

Figure 1. Procedures for selecting cells with attributes in closest overall agreement to those described from field measurements. Plot centre is indicated by star with the search routine moving in a clockwise direction as indicated arrows. The sequence from upper left to lower right is hierachical: (1st) aspect, (2nd) slope, (3rd) θ, and finally, repositioning of the plot. AWSC: Available Water Soil Capacity; DEM: Digital elevation model.

- This process is repeated on the slope layer with cells having values within ± 20% of the plot slope being tagged as acceptable candidates.
- All cells in the search region are then ranked based on the above classifications, with cells having two successful passes (i.e., both aspect and slope being within the specified thresholds) ranked the highest (code 3), followed by plots with aspects within specific thresholds but not slopes (code 2), cells with slopes correct but not aspect (code 1), and finally cells where neither the DEM slope nor aspect lays within the specified thresholds.
- Only cells with the maximum code are kept; all other cells are discarded. For all remaining possible candidates, the predicted θ of each cell is extracted and compared to the value of θ recorded at the plot. The cell with the highest code based on aspect and slope suitability and the smallest absolute difference between θ predicted by the DEM and measured in the field was then selected as the new plot position.

Implicit in this approach is a hierarchy in the application of the thresholds with plot aspect in this project selected as the most important terrain variable to match. This is primary due to the strong effect of aspect on radiation, especially at sites with high latitudes. For example, the incorrect positioning of the plot location based on aspect by locating it on an exposed rather than protected aspect, can have a major effect on its correct environmental description.

In this implementation, aspect and slope are first matched with the plot estimates. The comparison of θ is only undertaken in the final phase. As a result, if cells surrounding the original plot position have predicted θ values identical to those measured in the field and the slope and aspects do not lie within the selected thresholds, the cells are not candidates for plot selection.

The GIS-search algorithm was implemented at 2-boxcar filter sizes, the first with a maximum boxcar filter of 5 pixels from the plot center (equating to a maximum radius of 848 m from the original plot position) and a second, more conservative search limit with a maximum of 3 pixels from the plot center (equivalent to a maximum radius of 565 m from the original plot position). Statistical analysis was undertaken in the STATISTICA software package (StatSoft 1995).

Results

Extremes in elevation extracted from the DEM (with a cell resolution of 100 m) over the study area range from sea level (0 m) to 2840 m with a mean elevation of 850 m and a standard deviation of 507 m. This can be compared to the highest elevation in the study region (Mt. McLouglin at 2894m ASL). Figure 2(a) shows the frequency distributions of the field measured slopes of the 391 plots and the slopes extracted for the cells corresponding to the original plot positions. Figure 2(b) shows the frequency distribution of aspects for the 391 plots and the aspects extracted for all corresponding cells.

The two aspect distributions show similar trends with 1 or 2% differences in the number of plots in each of the 16 categories of aspect. Both distributions indicate that there are fewer plots located in an easterly than westerly direction. The most common field measured aspect was in a southerly direction, while the maximum number of cells from the DEM are located in northerly directions. The slope distributions are distinctly different with large variations in the number of plots in each of the slope-percentage classes. A major effect of the 100 m spatial resolution of the DEM is to impose a smoothing function on its representation of terrain, which results in many high frequency spatial features such as ridges and gullies being smoothed by the DEM algorithm at the 100 m cell scale. Consequently, slopes computed from the DEM are less steep than those measured in the field. Thus in Figure 2a DEM cells have slopes greater than 60 % yet 3 % of the 391 field plots have slopes exceeding 60 %. Therefore, there is a much greater percentage of cells from the DEM plots in the lower slope classes than estimated at each plot.

A Kolmogorov-Smirnov statistic provides a method to verify the similarity of the two distributions by testing if the samples are representative of the same distribution. The Kolmogorov-Smirnov assesses the hypothesis that two samples (the field data and the data extracted from the DEM) were drawn from different populations. The test is sensitive to differences in the general shapes of the distributions in the two samples and if the test is statistically significant results in the rejection of the hypothesis that the DEM data matches the field observations (Kolmogorov 1941). The test indicates that the distributions and the variances

(a)

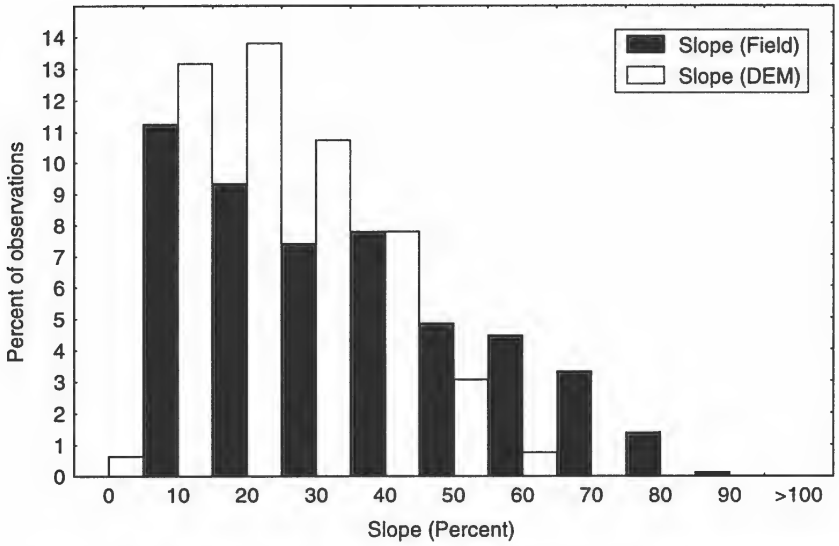

Figure 2a. Frequency distributions of slopes as measured in the field at their original locations and those derived from DEM.

(b)

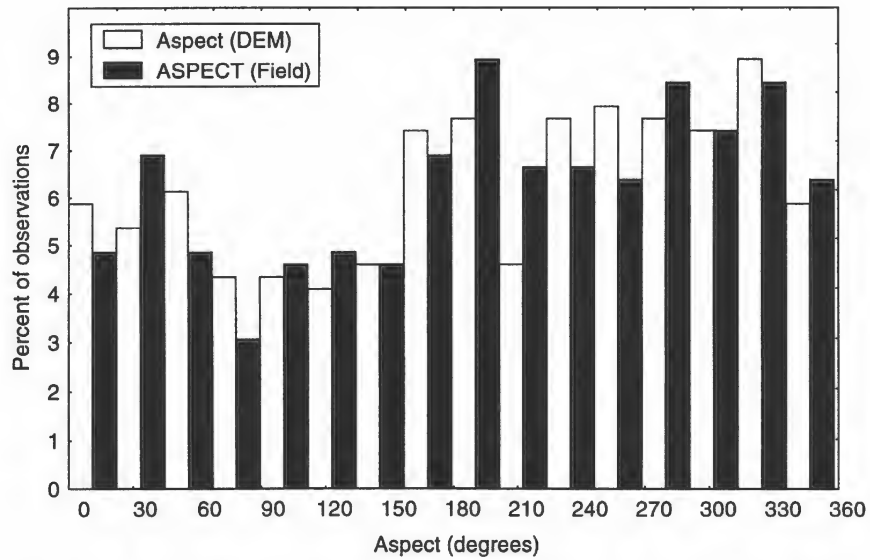

Figure 2b. Frequency distributions of aspect as measured in the field at their original locations and as derived from DEM.

of the DEM and plot data for both slopes and aspects are significantly different at the 0.05 level, with the differences in slope distributions and variances being highly significant ($P < 0.01$).

Figure 3a shows the field estimates of elevation (in meters) plotted against the elevation of the 391 cells correspond closely to values measured at the original plot locations. Figure 3b shows the field estimates of aspect (in degrees) plotted against the aspect of the 391 cells recorded at the original plot locations and Figure 3c for the slope estimates (in percent). These results indicate that while the elevations are in good agreement, the correspondence of DEM estimates of the slopes and aspects with data recorded at the 391 plots is poor, particularly for the latter attribute.

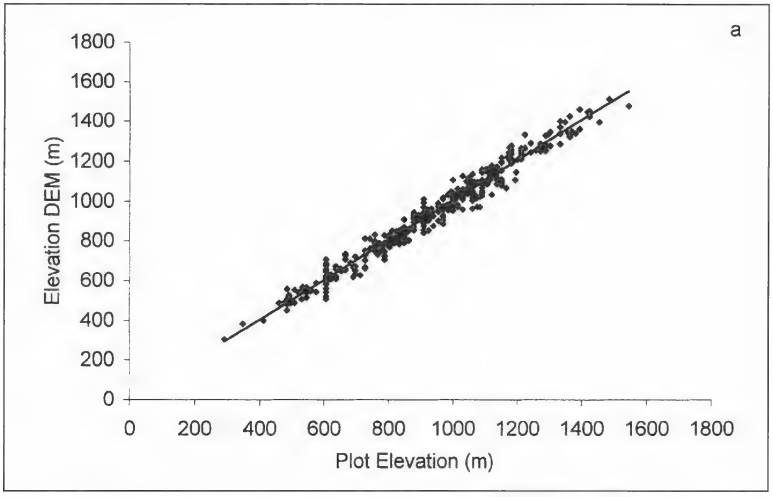

Figure 3a. Relationship between elevation recorded at the original locations in the field and that predicted with the DEM ($r^2 = 0.97$, DEM Elevation = 1.0 * Plot Elevation - 0.02, n=391, $P < 0.0001$)

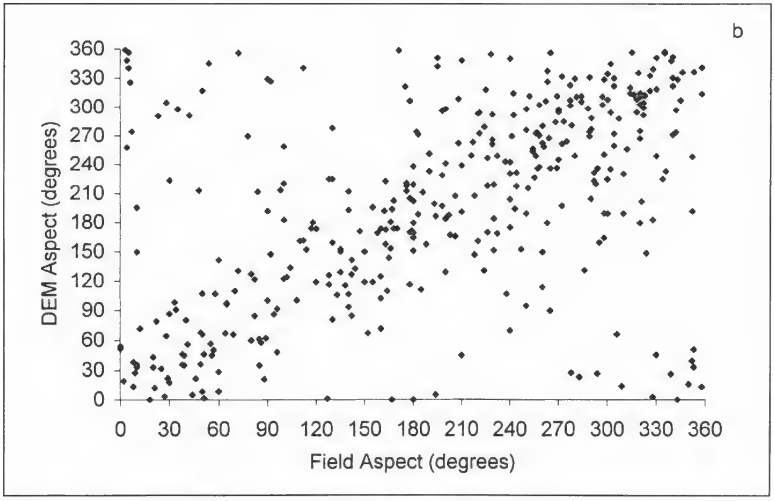

Figure 3b. Relationship between aspect recorded at the original locations in the field and that predicted with the DEM ($r^2 = 0.23$, DEM Aspect = 0.49 * Plot Aspect + 94.6, n=391, $P < 0.0001$)

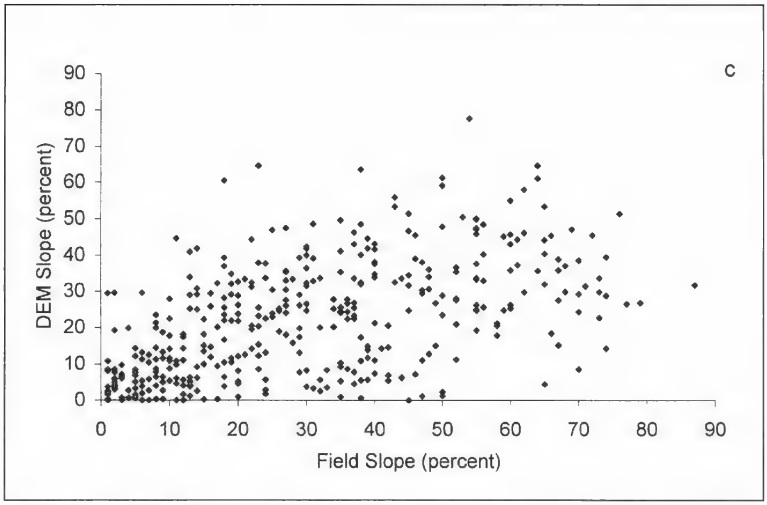

Figure 3c. Relationship between slope recorded at the original locations in the field and that predicted with the DEM (r^2 = 0.30, DEM slope = 0.42 * Plot Slope + 9.1, n=391, $P <$ 0.0001)

The good agreement between the elevations recorded at the plots and those extracted from the DEM indicate that, while the geographic location of the plots and the terrain cells may not directly correspond, the locations are generally within close proximity, and differences are mainly associated with local variations in slope and aspect.

Figures 4a and b show the relationship between the field aspects and DEM aspects in the new positions determined with the GIS-search algorithm. Two sets of results are presented using the 3-and the 5-pixel-radius-search boxcar filters. The figures show the hierarchy of the search procedure with the code 3, 2, and 1 results represented as different symbols. In a number of cases, the plot measured aspect and slopes could not be matched to any cells in the DEM search filters. In the 5 pixel radius, 3.3% of plots (n=13) could not be matched, with 3.6 % unmatched (n=14) using the 3 pixel radius. As a result, these plots were removed from the dataset and are not included in the presentation of the results.

Figures 4c and d show the relationship between the field slopes and the slopes of the DEM cells in the new positions determined using the GIS search algorithm. Again both sets of searches are presented and the figures show the hierarchy with the code 3, 2 and 1 identified. Figures 4e and f shows the predicted versus measured θ as extracted at new plot positions for both the 5-and 3-pixel-boxcar-search windows.

Figure 4a and b show that there is a significant increase in the correspondence between aspect measured at the plot and that at the repositioned plot locations extracted from the DEM. In the case of 5-pixel radius, the majority of the plots (84%) have been coded 3, which indicates that both the slope and the aspect of the repositioned plots were within the slope and aspect threshold classes. Additionally, 8% of plots were coded 2 which indicates aspect of the repositioned plots were within the threshold established although no cells with slopes within the prescribed threshold could be located. Because of the 360° representation of aspect, values < 22.5° or > than 347.5° transfer to the NE or NW quadrants; This results in their location appearing to be more erroneous than is actually the case on the scatter plot.

The distribution of plots with code 1 (plots with slope within the slope thresholds but no agreement with aspect) appears to be random over the range of aspect indicating that, in spite of matching slopes, there was a continual mismatch at some plots. The results of the larger search window (5 pixels) is a tighter clumping of the measured versus predicted aspects along the 1:1 line with more cells classified as code 3 and less as code 2 than resulted with the more conservative window. The

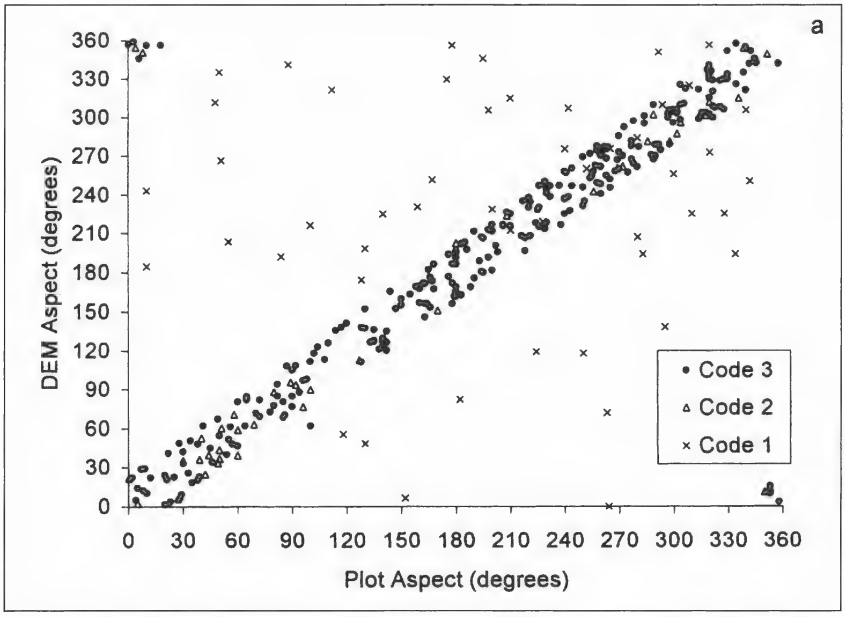

Figure 4a. Relationship between aspect recorded at the original locations in the field and that adjusted with the search routine for a 5 pixel radius window ($r^2 = 0.82$, DEM Aspect = 0.92 * Plot Aspect +11.4, n=391, $P < 0.0001$)

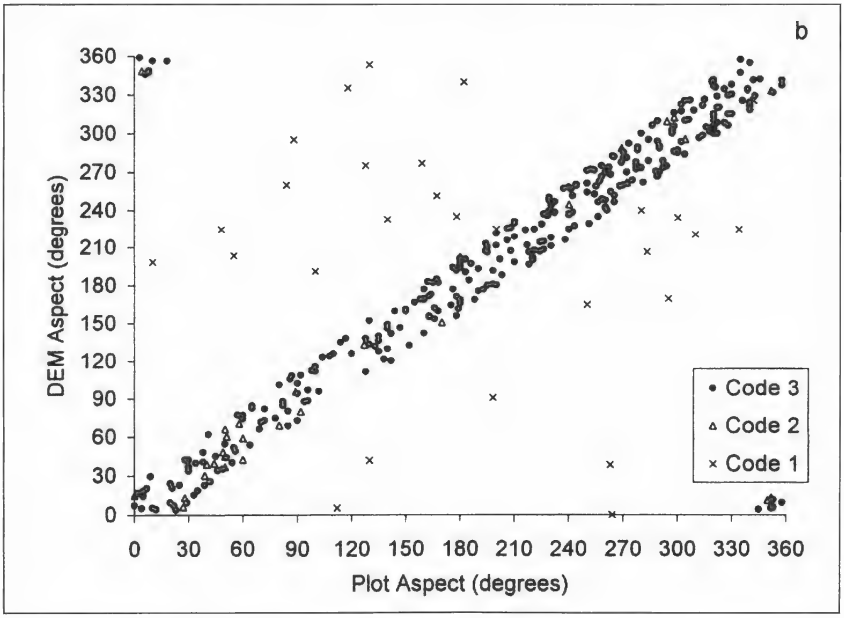

Figure 4b. Relationship between aspect recorded at the original locations in the field and that predicted with a 3 pixel radius window ($r^2 = 0.73$, DEM Aspect = 0.85 * Plot Aspect + 24.1, n=391, $P < 0.0001$)

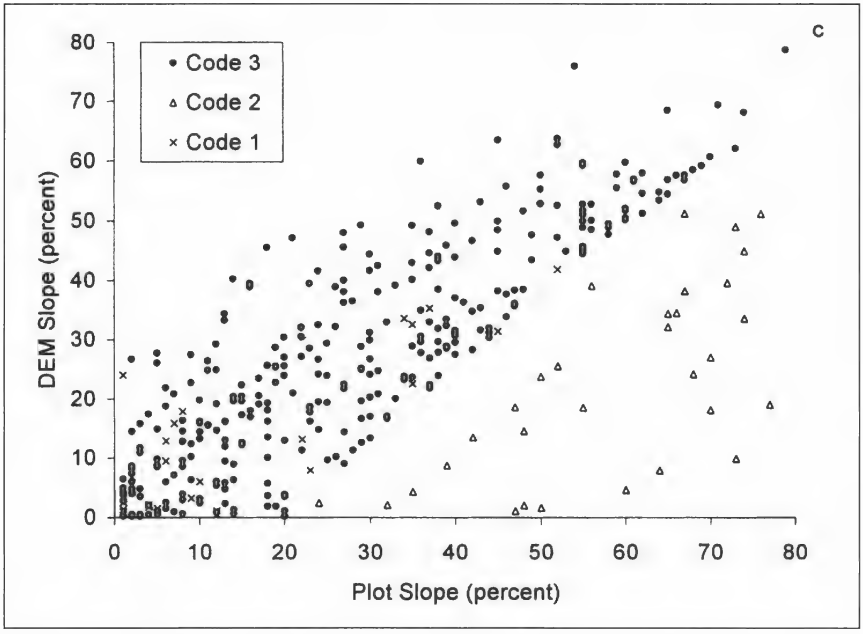

Figure 4c. Relationship between slopes recorded at the original locations in the field and that predicted with a 5 pixel radius window ($r^2 = 0.56$, DEM Slope = 0.67 * Plot Slope + 6.53, n=391, $P < 0.0001$).

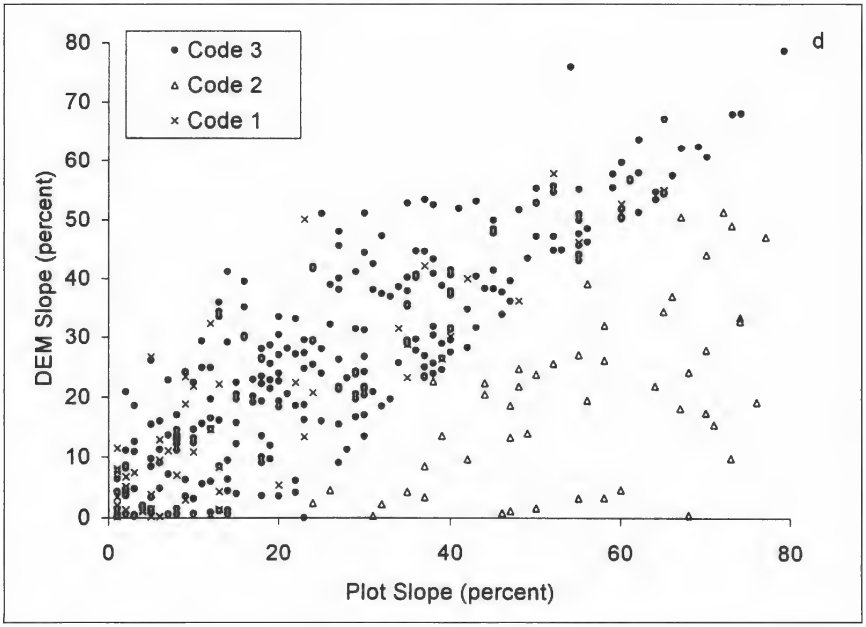

Figure 4d. Relationship between slopes recorded at the original locations in the field and that predicted with a 3 pixel radius window ($r^2 = 0.47$, DEM slope = 0.58* Plot Slope + 7.85, n=391, $P < 0.0001$)

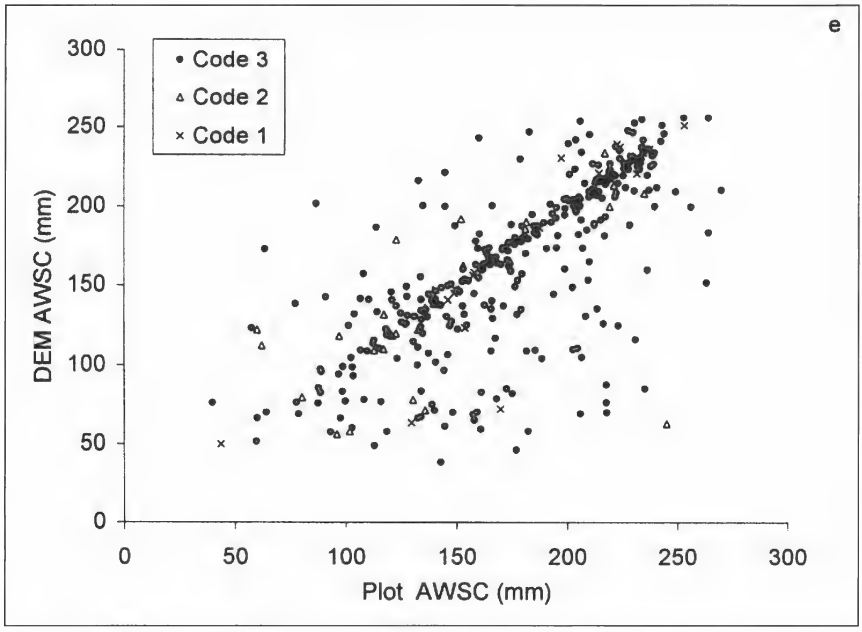

Figure 4e. Relationship between θ recorded at the original locations in the field and that predicted with a 5 pixel radius window ($r^2 = 0.54$, DEM θ = 0.63 * Plot θ + 69.5, n=391, $P < 0.0001$)

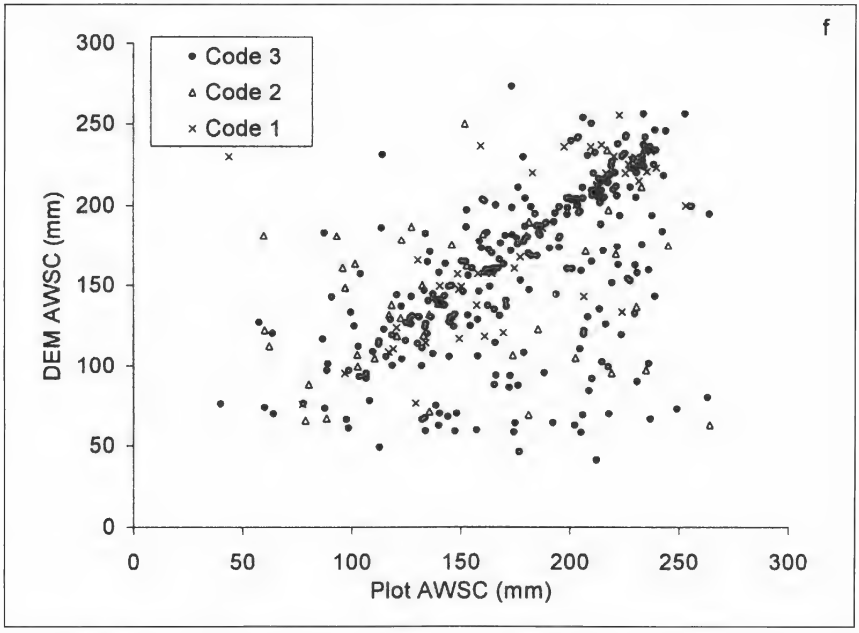

Figure 4f. Relationship between θ recorded at the original locations in the field and that predicted with a 3 pixel radius window ($r^2 = 0.27$, DEM θ = 0.47 Plot θ + 98.4, n=391, $P < 0.0001$)

percentage of plots that produced a code 1 (aspect incorrect, slope correct) (15% for the 5 pixel filter and 8% for the 3 pixel filter) indicates that the most of the plots more easily fell within the slope threshold than with the aspect thresholds.

Figure 4c and d indicate that, like the aspect comparison, there is a significant improvement in the agreement between measured slope and that extracted at the new locations from the DEM. The wider search window provides a slightly closer matching of the field observations with those derived with the DEM. With wider window, the codes 2 and code 1 assignments are also less frequent. The effect of topographic smoothing at 100m spatial resolution can be seen with an overall bias; a field-measured slope of 80% corresponds to approximately 70% on the 100m DEM.

Figure 4d and e show the relationship between the measured θ and that predicted by the DEM at the new cell positions using the search algorithm for both the 5 and 3 pixel boxcar windows. The results, as expected, are similar to the slope and aspect analysis with significantly improved relationships. The search with a 5-pixel radius produced a significantly tighter correspondence with the plots than that with a 3-pixel radius. This is expected as the algorithm in its final step attempts to minimize the difference between field estimates and modeled θ over all the cells with the maximum code value. Because the 5-pixel radius has a larger number of cells, a tighter relationship between the observed and predicted values results. There appears to be no significant pattern in the location of the code 2 or code 1 values in these figures. Overall, model predictions tend to underestimate θ values recorded in the field.

Figure 5 shows statistics on the distances required to move the original plot positions to locations where terrain attributes are in closer agreement. The distributions are shown for both the 3-and 5-window searches. Details of the distances can be seen in Table 3. Overall, the mean movement of the plots to their new location using the 5-pixel radius search window was 435 m and with the 3-pixel radius, 289 m (Table 3).

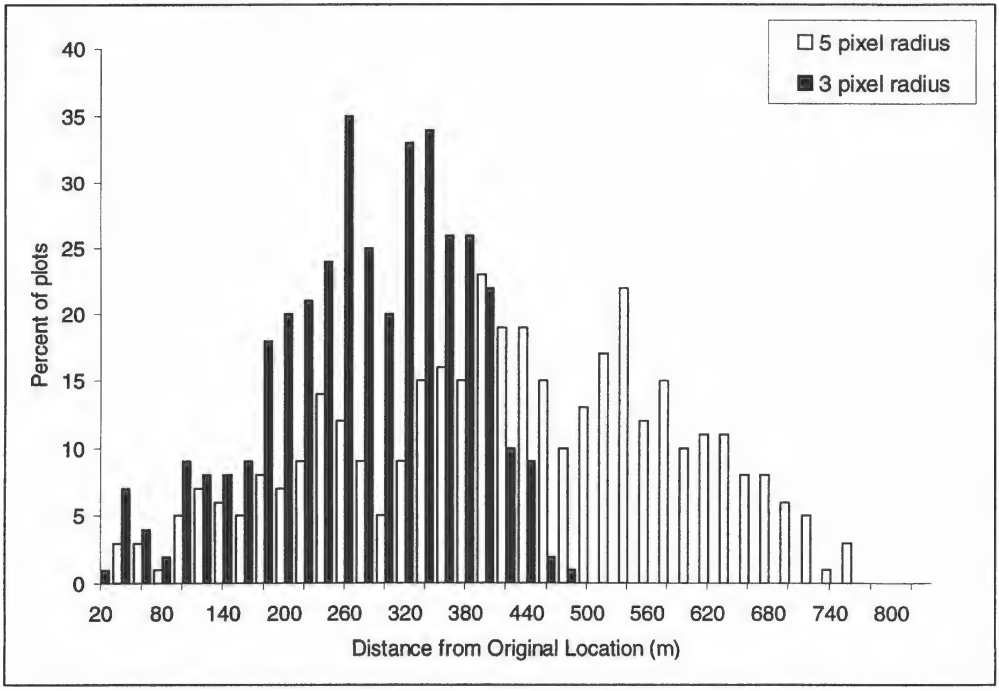

Figure 5. Histogram of distances moved from original locations of plots using 5 and 3 pixel radius windows respectively.

TABLE 3. Summary of distance statistics related to repositioning field plots using hierarchical search routine with two window sizes.

Size of Search Radius (pixels)	Maximum Distance (m)	Minimum Distance (m)	Mean Distance (m)	Variance of Distances (m)
5	749	25.5	412	165
3	461	14.8	269	95

Discussion

The hierarchical-search approach presented here provides an approach of repositioning plots, whose position was originally determined on different base maps and without access to global positioning technology. The approach relies on utilizing the large number of topographic and physiographic datasets that usually accompany field surveys.

As described in the introduction, DEMs are rarely without error and are often unavailable at the most appropriate scale (Hutchinson 1999). An inherent assumption of this technique is that the terrain attributes extracted from the DEM are realistic representations of the local terrain. Finer scale resolution DEM are currently becoming available over the continental U.S. with spatial resolutions of 30 m. Obviously, the techniques developed in this paper can be applied to these fine scale DEMs. An added benefit of utilizing these finer scale DEMs is the more accurate representation of fine scale topographic features such as slopes and gullies.

Given potential errors in both field location of plots and in the interpolation from DEM surfaces, the approach described in this paper provides a link between the two types of data sets by positioning the plots on the DEM, not by their absolute geographic locations but by attempting to match their recorded terrain environment as closely as possible. In many cases where extrapolation of climatic data and modeling of growth and distribution are involved, the actual geographic position of a plot is generally not as relevant as ensuring that the environmental regimes, which are correlated with terrain attributes, are similar. In the case of solar radiation, the aspect and slope are particularly critical, because assignment of a north slope to a south aspect with 25° slope at 45° Latitude results in a difference of more than 250 %. In such cases, the actual plot position on the DEM may be some hundreds of meters from the originally recorded plot position without introducing significant errors in modeling.

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Legacy Retention Versus Thinning: Influences on Small Mammals

Abstract

Management strategies for promoting late-seral attributes in second-growth forest need evaluation for their efficacy in maintaining biodiversity, including complete forest-floor, small-mammal communities. Two common strategies in the Pacific Northwest are (1) management with thinnings to promote large trees with developed understories and (2) retention of legacies, defined as live trees, logs, and snags from the preceding forest, at harvest, followed by protection but not thinnings of the new stand. We compared small-mammal communities resulting from >65 yr of application of these strategies in the Puget Trough, Washington. We also compared these communities with the small-mammal communities found in old-growth, naturally young, and extensively managed forests elsewhere in western Washington. Forests managed with thinnings had 1.5 times the individual mammals and 1.7 times the mammal biomass of forests managed with legacies of coarse woody debris and snags—differences similar to those between old-growth and naturally young forest (1.2 times more individuals in old-growth) and old-growth and extensively managed forest (1.6 times more individuals in old-growth). Management strategy had a profound impact on community structure, with the Columbian mouse (*Peromyscus oreas*), the small mammal most associated with old growth, much reduced in Puget Trough forests (absent from most stands) and the creeping vole (*Microtus oregoni*) (a species commonly associated with early seral stages, but found in all seral stages in Washington) third-ranked in thinned stands but seventh ranked in legacy stands. The montane shrew (*Sorex monticolus*) was second-ranked, after Trowbridge's shrew (*S. trowbridgii*), in marked contrast to codominance by the southern red-backed vole (*Clethrionomys gapperi*), *S. monticolus,* and *P. oreas* in old growth. Thus, neither strategy produced communities typical of late-seral forests.

Introduction

Harvest of Pacific Northwest old growth has raised questions concerning the ability of younger, managed stands to adequately sustain wildlife diversity and abundance (Meslow et al. 1981; Carey 1989; Thomas 1991; Carey et al. 1992). Ecologists warned decades ago that harvest-regenerated, densely stocked, unthinned, coniferous forests and forests lacking snags and coarse woody debris were detrimental to small-mammal populations (Hamilton and Cook 1940). Clearcutting in the Pacific Northwest created extensive tracts of forest with various levels of these conditions. Second-growth stands often have few old, large, snags, logs, and trees (hereafter referred to collectively as legacies), reduced vertical and horizontal heterogeneity in vegetation structure, and diminished ecological function (Carey et al. 1996*b*).

The rate of clearcutting in the Pacific Northwest has slowed during the past decade (McGinnis et al. 1997), and new forestry techniques presumed to have fewer esthetic and ecological drawbacks have emerged (Franklin 1989; Hansen et al. 1995; Carey et al. 1996*a*; Curtis and Carey 1996). Two of the most commonly recommended (and potentially opposing) alternatives for managing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests are multiple thinnings and legacy retention (snags, logs, live trees) at harvest (Franklin et al. 1981; Carey and Curtis 1996; Carey et al. 1996*a*; Hayes et al. 1997; Tappeiner et al. 1997). Management by thinning combines multiple commercial thinnings with long rotations to produce stands with large contemporary trees and developed understories. As these stands mature, they are hypothesized to develop the functions and processes of late-seral forest (Weigand et al. 1993) and accrue commercial value as timber (Perry 1998). Legacy retention emphasizes retaining biologically significant structures (logs, snags, live trees) and intact patches of forest floor at final harvest to provide structures and sources for colonization of the new stand by organisms of limited mobility. Harvest under legacy management systems leaves standing trees—both healthy and decadent, in patches or singly—up to 30% of the stand basal area although standard guidelines have not been set (Franklin et al. 1997). Thinning is precluded under this management strategy. The resulting closed-canopy stands inoculated with snags, logs, and older trees are hypothesized to foster biodiversity similar to a late-seral forest

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(Hopwood 1991; Franklin 1993; Franklin et al. 1997). Both of these strategies have been suggested in forest management literature and in habitat conservation plans (e.g., FEMAT 1993). However, the long-term ecological effects of these techniques are virtually unknown.

We compared small-mammal communities resulting from 65 years of application of the two strategies to second-growth stands in the Puget Trough of Washington. First, we examined small-mammal abundances. Because small mammals are generally more abundant in old growth than in extensively managed second growth (Carey and Johnson 1995), we were interested in the relative potential of thinning versus retention of old, large, snags, logs, and live trees to produce abundances of small-mammals in second growth. Only species with niche dimensions (Carey 1981; Carey et al. 1999*a*) affected by thinning or legacy retention would be expected to be influenced by the two management strategies. We hypothesized that the shrew-mole (*Neurotrichus gibbsii*) and Trowbridge's shrew (*Sorex trowbridgii*) would be more numerous under legacy management and its concomitant retention of coarse woody debris, and that deer mice (*Peromyscus maniculatus*) and creeping voles (*Microtus oregoni*) would be more abundant under thinning management and its resulting understory development (Carey and Johnson 1995). Of particular interest was the Columbian mouse (*P. oreas*), a species tied to old growth (West 1991; Carey and Johnson 1995; Songer et al. 1997). The Columbian mouse seems associated with tall understory and, perhaps, shade-tolerant midstories; we expected this mouse to be more abundant in the thinned forest. Although the mycophagous southern red-backed vole (*Clethrionomys gapperi*) is positively correlated with both coarse woody debris and shrubs (Carey and Johnson 1995), we expected higher abundances under legacy management because of the fungal-food resources associated with coarse woody debris (Maser et al. 1978). In addition to examining abundances, we calculated reproductive statistics to ensure we did not confound abundances with variation in population demographics (Van Horne 1983).

Second, we compared diversity and community structure (species rank abundances) under thinning and legacy management to diversity and structure in old-growth, naturally young, and extensively managed forests in the adjacent physiographic provinces (Olympic Peninsula and southern Washington Cascades)–no data on small mammals in old-growth or naturally young forests in the Puget Trough were available. We used these comparisons to evaluate the likelihood that either active management strategy would produce complete communities with abundant small mammals.

Methods

Study Area

Our study sites were on the Fort Lewis Military Reservation, 30 km northeast of Olympia in Thurston County, Puget Trough Physiographic Province, Washington (Franklin and Dyrness 1973). Due to its extensive forest cover and strategic location between the large federal land holdings on the Olympic Peninsula and in the Cascade Range, Fort Lewis was named a Designated Conservation Area for the Northern Spotted Owl (Lujan et al. 1992). The area is composed of about 6,000 ha of second-growth Douglas-fir stands with various management histories. Large tracts of homogeneous stands and the U.S. Army's desire to reconcile land management objectives for timber with conservation of threatened species made the area ideal for comparing forests of differing management histories (Carey et al. 1999*b*).

We had four study sites. Two sites were managed by thinning and two were managed by legacy retention without thinning. Each site had four stands. We randomly selected two stands per site. Stands were separated by a minimum of 200 m within study sites and we considered stands independent because the number of forest-floor small-mammal movements between stands was negligible. All study sites were seed-regenerated after clearcutting and dominated by second-growth Douglas-fir. Trees were fewer and larger, understory more abundant, and coarse woody debris less in thinned stands than in legacy stands (Carey et al. 1999*b*).

Thinned sites were clearcut ~1927 and thinned 45 years and 62 years after clearcutting. Commercial thinning operations removed subordinate, merchantable live, dead, and diseased trees, and salvageable fallen trees. Each thinning removed 17.5 - 33.8 m^3/ha. Few snags and scant coarse woody debris remained. Thinning produced large (52-cm dbh) Douglas-fir, a low shrub layer typified by salal (*Gaultheria shallon* Pursh), and a patchy herbaceous layer. Stand condition resembled

the understory reinitiation stage described by Carey and Curtis (1996).

Sites managed with legacy retention were clearcut ~1937, and numerous large trees, snags, logs, and stumps were left on site following harvest. The stand was left to reestablish and grow naturally resulting in heavy stocking with small-diameter Douglas-fir. The forest floor had moderate accumulations of dead, small-diameter trees from the current cohort of trees and large coarse woody debris from the original old-growth forest. Shrub height was low (<0.5 m) and moss was more extensive than herbaceous ground cover. Later (ca. 1981), a small number of standing legacy trees that projected above the canopy and were deemed a hazard to military aircraft were felled and left on the forest floor. Stand development closely resembled the competitive-exclusion stage (Carey and Curtis 1996).

Sampling Procedures

In each stand we established a 10 x 10 trapping grid with 20-m spacing between grid points. Each trapping grid encompassed 4 ha. We visually estimated cover of down wood and low vegetation on 4-m-radius plots (50-m^2) centered on grid points (n = 100 plots per stand). We estimated percent cover for small woody debris 5-15 cm in diameter; coarse woody debris > 15 cm in diameter; herbs, including ferns; and shrubs; and shrub height <2 m. Plots encompassed 13% of each grid. Additional sampling included 15 variable-radius prism plots (basal area factor 30 English) to determine tree dbh for each grid (Carey et al. 1999*b*).

Two Sherman live traps (Sherman Co., Tallahassee, Fl.), one large (7.6 cm x 8.9 cm x 22.9 cm) and one small (5.1 cm x 6.4 cm x 16.5 cm), were placed at least 1 m apart within 2 m of each grid point. Traps were checked and treadle tension was adjusted daily to ensure that traps operated freely and could capture even the lightest insectivores (<4 g). Traps were baited with a mixture of peanut butter, whole oats, and molasses. Polyester batting was placed in each trap to provide thermal insulation and bedding material for trapped animals. We recorded species, age, sex, reproductive status, weight (g), and capture status (new capture or recapture) for each captured mammal. We recorded all sprung traps. A single Monel eartag (National Band and Tag Co.) was attached to the right ear of mice, voles, and squirrels. Insectivores were not marked because most died as a result of trapping. We used tail length to distinguish between species of *Peromyscus*. *Peromyscus* with tails >96 mm were designated as Columbian mice, and shorter-tailed animals were designated as deer mice (Allard et al. 1987). Classification of mice and voles as adult or young was based on weight and external criteria indicative of reproductive condition (McCravy and Rose 1992). Mice and voles in breeding condition or showing signs of past breeding were classified as adults. Otherwise, deer mice that had not attained the brownish pelage of adults, and deer mice and voles < 15 g, were considered to be young of the year. Each animal that died was collected for necropsy to confirm species, sex, and reproductive status. Morphology of the median tine (Carraway 1995), tail length, and pelage characteristics were used to identify shrew species. Shrew age (adult or young) was determined by the amount of tooth wear on incisors and unicuspids (Rudd 1955; Hawes 1977). Where necropsy samples allowed, mean litter size was determined by species for each management strategy. Taxonomy and nomenclature follow Jones et al. (1992).

All grids were trapped for forest-floor small mammals during three consecutive summers (1992-1994). Repeated sampling was undertaken because we expected significant interannual fluctuations in mammal populations. We selected summer trapping (mid-July to mid-August) to coincide with peak numbers of forest-floor small mammals and to allow data collection on multiple age and breeding classes. We trapped small mammals in two consecutive trapping sessions of eight nights each; one-half the stands under each management strategy were trapped in each session.

Data Analysis

We calculated descriptive statistics to determine the need for transformations and appropriateness of parametric tests. Summary statistics of means and standard errors are reported. The biological significance of test results was evaluated when statistical significance was $P \leq 0.05$. We used arcsine square root transformations for habitat variables (except dbh) and performed t-tests using four samples per management strategy (Bonham 1989; Carey and Johnson 1995). The forest-floor small-mammal community was defined as the

assemblage of mice (*Peromyscus maniculatus* and *oreas*), voles (*Clethrionomys gapperi* and *Microtus oregoni*), shrews (*Sorex trowbridgii, S. monticolus, S. vagrans*), and shrew-moles (*Neurotrichus gibbsii*) that normally occur on upland sites and that we caught regularly in our traps. We excluded the marsh shrew (*S. bendirii*) because it is primarily associated with damp areas (Ingles 1965) and the Pacific jumping mouse (*Zapus trinotatus* Rhoads) because it is associated with meadows (Ingles 1965) and riparian areas (Doyle 1985). Moles (*Scapanus spp.*) were excluded because they were not routinely captured by our traps.

The sampling unit was the stand, and the primary response variable was animal abundance by species by year. We assumed that probability of capture was equal between management strategies. For each species we calculated total individuals captured per 100 trap nights (CPU) corrected for traps sprung by any cause (Nelson and Clarke 1973; Carey et al. 1999*a*). We used a transformed measure [ln (CPU + 1)] to compare species abundances (Carey and Johnson 1995) between management strategies and among years with a simple factorial ANOVA with a year x management strategy interaction (Norušis 1993). One could argue repeated-measures ANOVA was appropriate here; we conducted such an analysis and found comparable results. Tukey's honestly significant difference test was used for post hoc multiple comparisons among years (SPSS 1997). We also plotted mean annual CPU for each species by management strategy. We then inspected plots for synchrony in annual fluctuations (Boonstra et al. 1998) among species and between management strategies.

Because density has been questioned as an appropriate indicator of habitat quality (Van Horne 1983), we determined demographic statistics for each population based on sex ratio, age ratio, and the proportion of the population composed of reproductive females. We used these vital rates to determine if we were dealing with source populations which are self replacing and sink populations which are receptacles of the surplus from nearby sources. We counted females showing signs of lactation, pregnancy, or estrus to determine the proportion of the population composed of reproductively active females. Mann-Whitney U tests were used to determine if there were significant rank differences in species age ratio, sex ratio, or proportion of the population composed of reproductive females between thinned and legacy treatments. For each species, we multiplied number of individuals caught (Krebs 1966) by mean body-mass and used a Mann-Whitney U test to determine if there were significant differences in biomass between management strategies.

To compare small-mammal community diversity—species richness and evenness—between management strategies and across the three years of our study, we used the Shannon index. We calculated an index value for each stand by year (n = 24), then found the mean index value for each of our eight stands. We used the eight Shannon index values, four per management strategy, in a t-test (Magurran 1988).

Inter-regional Comparisons

We compared small-mammal community structure on our sites to those found in old-growth and young forests on the Olympic Peninsula and the southern Washington Cascades. The effect of stand conditions on species abundances were not directly comparable between regions due to differences in trapping methods and significant interannual variation in animal abundances. However, the index of abundance (CPU) based on individual captures and relative frequencies served as corrective factors allowing us to generate regional small-mammal community structures by ranking adequately sampled species by abundance (Carey et al. 1991, Carey and Johnson 1995). In Puget Trough forests, CPUs were derived as stated above. In the southern Washington Cascades, CPU was derived by taking the mean of two years' (1984 -1985) combined snap trap and pitfall trap data presented by West (1991). Olympic Peninsula CPUs were taken directly from snap trap data, 1987 -1989, presented by Carey and Johnson (1995).

Results

Habitat Attributes of Management Strategies

Commercially thinned stands had trees with significantly larger diameters (t = -15.50, df = 6, P < 0.001) and significantly taller shrubs (t = -4.10, df = 6, P = 0.006) than legacy stands (Table 1). Herb cover (t = -2.35, df = 6, P = 0.057) and shrub volume (t = -2.36, df = 6, P = 0.056) were marginally greater under the thinning management

TABLE 1. Mean, range, and 95% confidence interval (CI) of habitat values for stands managed by retaining logs, snags, and residual trees from the previous stand and stands managed by thinning in the Puget Trough, Washington, 1992-1994.

	Legacy stands n = 4			Thinned stands n = 4		
Habitat feature[1]	Mean	Range	CI	Mean	Range	CI
Dbh trees (cm)	35	29-37	29-42	52	48-60	43-61
SWD (%)[2]	3	2-5	1-5	1	<1-2	0-2
CWD (%)[3]	6	5-9	3-10	1	<1-2	1-2
Herb cover (%)	4	2-7	1-7	10	5-16	2-18
Shrub cover (%)	16	12-20	10-21	21	13-27	10-32
Shrub height (%)[4]	23	20-26	19-27	32	28-36	26-37

[1]Stand values based on 100 sampling points per stand.
[2]Forest floor small woody debris <15 (cm) and > 5 (cm) in diameter.
[3]Forest floor coarse woody debris >15 (cm) in diameter.
[4]Shrub height expressed as % of 2 m.

strategy. However, mean shrub cover did not differ significantly ($t = -1.28$, $df = 6$, $P = 0.249$) between management strategies. Legacy stands had a significantly greater cover of coarse woody debris ($t = 5.41$, $df = 6$, $P = 0.002$) and small woody debris ($t = 3.70$, $df = 6$, $P = 0.010$) than thinned stands.

Mammal Abundance and Distribution

We caught 4,280 individual small mammals of 16 species (Table 2). Six species, Trowbridge's shrew, montane shrew (*S. monticolus*), southern red-backed vole, deer mouse, creeping vole, and shrew-mole accounted for 94% of total individuals trapped, and each of these species composed at least 3% of the individual small mammals trapped per management strategy. Trowbridge's shrew was the most numerous species under both strategies and occurred in every stand every year, as did montane shrews, red-backed voles, and deer mice. We caught 1.4 times as many individual small mammals in thinned stands as in legacy stands (Table 2). Contrary to our predictions, however, we found no difference in the abundances of red-backed voles, Trowbridge's shrews, and shrew-moles between strategies (Table 3). No species was statistically more abundant in the legacy stands. As we predicted, deer mice and creeping voles, and montane shrews as well, were more abundant in thinned stands. We had not expected to catch many squirrels, so we made no predictions. Never less, Northern flying squirrels (*Glaucomys sabrinus*) were captured four times more frequently in legacy stands than in thinned stands; however Townsend's chipmunks (*Tamias*

TABLE 2. Total individuals captured in 4 young stands managed by retaining logs, snags, and residual trees from the previous forest and 4 managed by repeated thinnings, Puget Trough, Washington, 1992-1994.

Species	Legacy retention	Intensive thinning	Total
Sorex trowbridgii	640	596	1236
Sorex monticolus	376	557	933
Clethrionomys gapperi	266	317	583
Peromyscus maniculatus	110	308	418
Microtus oregoni	51	407	458
Neurotrichus gibbsii	201	178	379
Sorex vagrans	57	31	88
Peromyscus oreas	6	12	18
Tamias townsendii	21	75	96
Glaucomys sabrinus	22	5	27
Mustela erminea	5	15	20
Mustela sp.	2	2	4
Peromyscus sp.	3	3	6
Scapanus orarius	1	1	2
Sorex bendirii	3	1	4
Mus musculus	2	0	2
Zapus trinotatus	0	3	3
Sorex sp.	1	1	2
Tamiasciurus douglasii	0	1	1
Total individuals	1767	2513	4280
Sprung traps[1]	1229	1709	2938
Trap nights	19200	19200	38400
CPU[2]	10	15	12

[1]Sprung traps includes repeat captures.
[2]Catch per 100 trap-nights, corrected for traps closed by any cause (Nelson and Clarke 1973).

TABLE 3. Results from an analysis of variance of small mammal abundances (ln [CPU + 1]) by management, year, and management x year interaction in 4 stands managed for logs, snags, and carried over residual trees, and 4 stands managed with repeated thinning, Puget Trough, Washington, 1992–1994.

Species	Legacy		Thinned		Management			Year			Year x management		
	$\bar{x}$	(se)	$\bar{x}$	(se)	F	df	P[1]	F	df	P[1]	F	df	P[1]
Sorex trowbridgii	1.52	(.05)	1.49	(.05)	0.2	1, 23	0.690	0.3	2, 23	0.761	0.01	2, 23	0.994
Sorex monticolus	1.12	(.06)	1.42	(.08)	11.3	1, 23	0.003	3.8	2, 23	0.041	0.1	2, 23	0.868
Clethrionomys. gapperi	0.88	(.09)	1.00	(.11)	0.9	1, 23	0.360	4.0	2, 23	0.036	2.9	2, 23	0.084
Neurotrichus gibbsii	0.72	(.09)	0.65	(.11)	0.2	1, 23	0.658	1.2	2, 23	0.314	0.6	2, 23	0.565
Peromyscus maniculatus	0.43	(.10)	0.98	(.11)	78.1	1, 23	0.000	49.3	2, 23	0.000	6.9	2, 23	0.006
Microtus oregoni	0.23	(.07)	1.16	(.11)	69.1	1, 23	0.000	5.8	2, 23	0.012	0.1	2, 23	0.945
Sorex vagrans	0.26	(.06)	0.15	(.05)	2.5	1, 23	0.133	5.3	2, 23	0.016	0.02	2, 23	0.982
Peromyscus oreas	0.03	(.02)	0.06	(.03)	0.7	1, 23	0.409	0.2	2, 23	0.835	0.2	2, 23	0.838

[1] Bold type indicates significance at $P \leq 0.05$.

townsendii) were >3 times more abundant in the thinned stands. Coast moles (*S. orarius*) and marsh shrews were captured infrequently under both management strategies. We captured the house mouse (*Mus musculus*) only in legacy stands and jumping mice only in thinned stands.

We did not predict that some usually common species would be absent from some stands. Creeping voles were absent from one legacy stand in 1992 and two in 1993. Shrew-moles were absent from one legacy stand in 1993. The vagrant shrew composed 3% of total individuals under legacy management and 1% under commercial thinning, and was absent from two thinned stands during 1992 and one thinned stand during 1993. Columbian mice were trapped only in the same two stands, one in each strategy, each year, except that a single Columbian mouse was captured on a second thinned grid during 1993. Columbian mice were restricted in distribution within the two occupied stands, occupying the same area from year to year.

Temporal Variation in Small-Mammal Abundance

Deer mice varied among years differently between management strategies (significant interaction effect) (Table 3). Deer mice, creeping voles, montane shrews, vagrant shrews, and shrew-moles all attained their highest mean abundance during 1994 under both management strategies (Figure 1). The highest mean abundance of red-backed voles in thinned stands also occurred during 1994 (Figure 1). Deer mice and vagrant shrews were more abundant in 1994 than in 1992, and deer mice were more abundant in 1992 than in 1993. During years with low mean abundance in legacy stands, confidence intervals encompassed 0 for creeping voles and approached 0 for deer mice, suggesting extirpations were possible (Figure 1). Similarly, confidence intervals for vagrant shrews encompassed 0 under each management strategy during years of low mean-abundance.

Population Structure and Biomass

Reproductively active females were ≤37% of individual captures for any species under both management strategies (Table 4). Necropsy of 1,226 animals from legacy stands yielded 27 pregnant females and necropsy of 1,422 animals from thinned stands yielded 69 pregnant females. Pooled data showed no significant differences in litter sizes between strategies (Mann-Whitney U test, $P \geq 0.15$; Table 4). We lacked sufficient samples to determine litter sizes for deer mice, Columbian mice, and shrew moles. We found greater proportions of adults in Trowbridge's shrew populations in thinned stands than in legacy stands (Table 4); however, the magnitude of the difference was small. There were no significant differences between management strategies in population sex ratios or proportions of reproductively active females for any species (Table 4). Total small-mammal biomass was 1.7 times as great in thinned stands as in legacy stands (Table 5).

Community Structure and Diversity

Small-mammal communities developed under the two strategies were dominated numerically by Trowbridge's shrews and montane shrews.

TABLE 4. Small mammal abundance, litter size, and Mann-Whitney U tests (*P*) for the effects of forest management strategy on population proportion of reproductively active females, sex ratio, and age ratio in four 4-ha sampling plots in each of two forests on Fort Lewis, Washington, 1992–1994.

		CPU[2]		Litter size[3]		Rpro-fem[4]			Sex M:F			Age A:Y		
Species	Mgmt[1]	$\bar{x}$	(se)	$\bar{x}$	(se)	$\bar{x}$	(se)	*(P)*	$\bar{x}$	(se)	*(P)*	$\bar{x}$	(se)	*(P)*
C. gapperi	L	1.5	(0.2)	2.4	(0.5)	0.20	(0.04)	0.36	2.9	(0.6)	0.45	5.2	(0.9)	0.21
	T	1.9	(0.3)	2.5	(0.2)	0.25	(0.04)		2.4	(0.4)		7.2	(1.0)	
M. oregoni	L	0.3	(0.1)	2.0	(1.0)	0.17	(0.08)	0.06	0.8	(0.2)	0.16	3.6	(1.4)	0.31
	T	2.4	(0.4)	2.5	(0.1)	0.33	(0.03)		1.4	(0.1)		4.8	(1.1)	
P. maniculatus	L	0.6	(0.2)	...	...	0.20	(0.05)	0.33	1.6	(0.2)	0.28	1.4	(0.3)	0.07
	T	1.8	(0.3)	...	...	0.26	(0.03)		2.1	(0.3)		2.4	(0.3)	
S. trowbridgii	L	3.6	(0.2)	3.0	(0.0)	0.20	(0.03)	0.69	1.2	(0.1)	0.42	0.5	(0.0)	0.01
	T	3.5	(0.2)	4.0	...	0.17	(0.02)		1.4	(0.1)		0.7	(0.0)	
S. monticolus	L	2.1	(0.2)	3.9	(0.3)	0.16	(0.02)	0.23	2.5	(0.4)	0.31	1.9	(0.3)	0.95
	T	3.3	(0.3)	3.6	(0.3)	0.19	(0.02)		1.8	(0.1)		1.9	(0.1)	
N. gibbsii	L	1.1	(0.2)	...	...	0.19	(0.03)	0.90	1.3	(0.3)	0.31	3.3	(1.2)	0.55
	T	1.1	(0.2)	3.0	...	0.20	(0.05)		1.5	(0.3)		2.1	(0.5)	
S. vagrans	L	0.3	(0.1)	4.0	(1.0)	0.32	(0.09)	0.93	1.0	(0.1)	0.78	1.2	(0.2)	0.90
	T	0.2	(0.1)	3.0	...	0.37	(0.14)		0.8	(0.1)		1.2	(0.2)	
P. oreas	L	0.03	(0.0)	...	...	0.25	(0.25)	1.00	0.00	...	0.08	0.7	(0.7)	0.6
	T	0.1	(0.0)	...	...	0.25	(0.16)		1.8	(0.7)		1.5	...	

[1] Management strategy, (L) retention of legacies of large logs, dead trees, and live trees and (T) thinning.

[2] Catch per 100 trap-nights corrected for traps closed by any cause (Nelson and Clarke 1973).

[3] Mean number of fetuses per female for each management strategy; of 2648 necropsies, 96 were pregnant females.

[4] Proportion of individuals captured that were reproductively active females, either in estrus, pregnant, lactating, or post lactating.

Community structure, however, differed significantly between the two strategies (Figure 2), with creeping voles being third ranked in thinned stands, but seventh ranked in legacy stands. Shrew-moles assumed greater importance in legacy communities than in thinned communities but were not significantly different in abundance between strategies. Community structure based on biomass (Table 5) differed from structure based on abundance. In thinned stands, the three common rodents—creeping vole, red-backed vole, and deer mouse—superseded the common shrews—Trowbridge's shrew and montane shrew—when community structure was based on biomass. In legacy stands, however, only red-backed voles superseded Trowbridge's shrew in biomass rank (Table 5). Deer mice, creeping voles, and montane shrews were significantly more abundant numerically and in biomass in thinned stands compared to legacy stands.

The same eight species composed the small-mammal communities in both legacy and thinned stands; only six species, however, occurred consistently in thinned stands and only five species in legacy stands (Figure 1). According to the Shannon index, the greater number of individuals in the thinned stands were more evenly distributed over species (H' = 1.68) than in the legacy-stand small-mammal communities (H' = 1.53) (t = -2.44, df = 6, P = 0.051).

Discussion

Small-Mammal Communities

Overall, the same species composed the forest-floor small-mammal communities in the thinned stands, legacy stands, old-growth and naturally young forest in the Southern Washington Cascades, and old-growth and extensively managed second-growth forests on the Olympic Peninsula (Figure

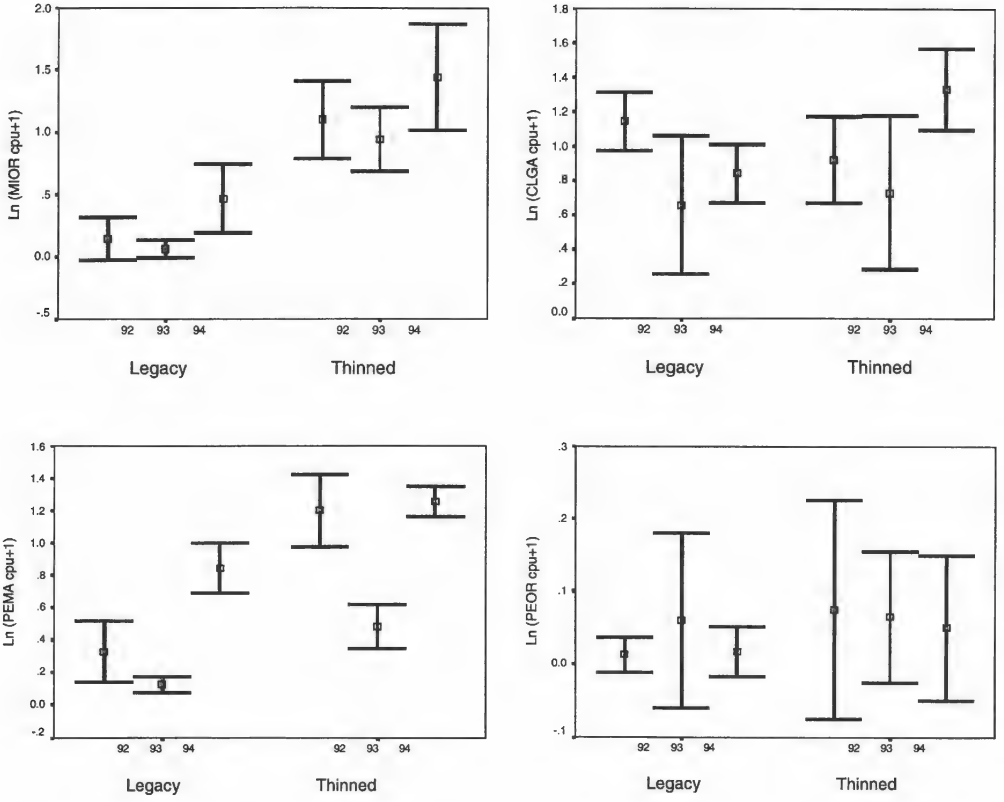
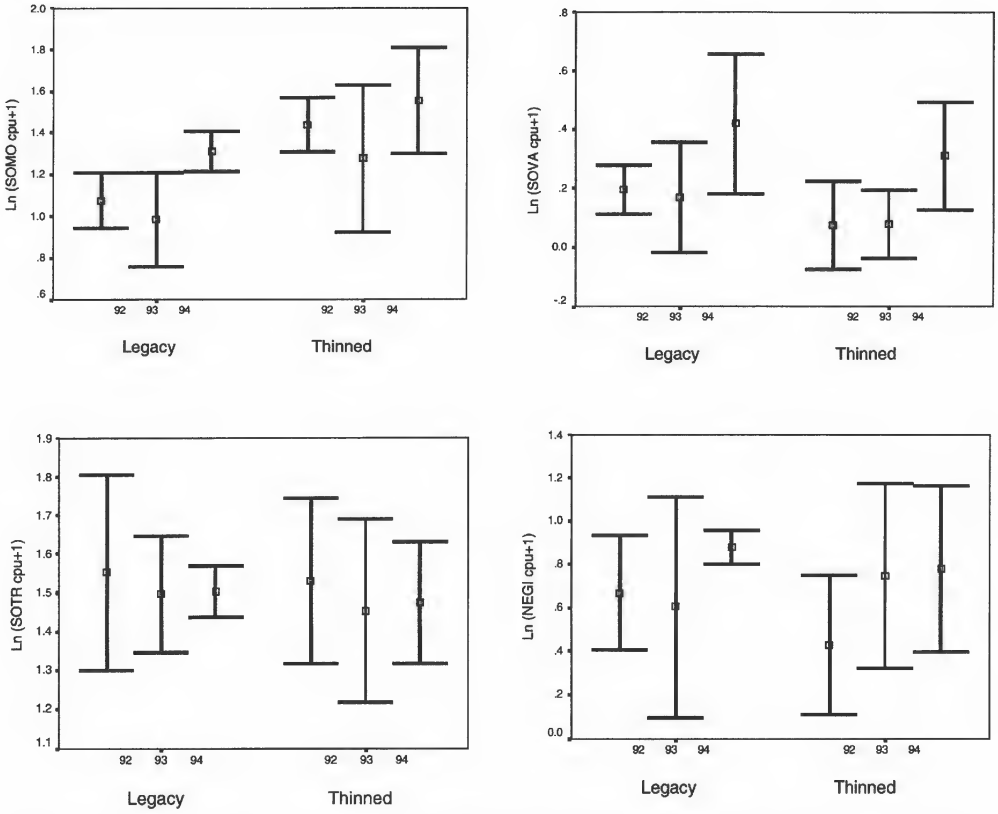


Figure 1. Error bars of small mammal abundance [Ln (CPU+1) ± 2*SE*] by year and management strategy in forest managed with letters of genus and species: *Clethrionimys gapperi, Microtus oregoni, Neurotrichus gibbsii, Peromyscus maniculatus,*

2). Although thinned stands had greater abundance, biomass, and diversity of small mammals than legacy stands, neither management strategy produced environments that consistently supported complete small-mammal communities when compared to old-growth forests in neighboring physiographic provinces. Small mammals were 1.2 and 1.6 times as abundant in old-growth as in natural young or managed young forest in the southern Washington Cascades and on the Olympic Peninsula, respectively (Carey and Johnson 1995). This difference was comparable to the differences that we found between thinning and legacy management strategies. Because small mammals feed widely on truffles (Ure and Maser 1982), invertebrates, and seeds (Gunther et al. 1983), the reported depression of these food resources in certain young managed forests (Buchanan et al. 1990; Carey 1991; Estrada-Venegas 1995; North et al. 1997) may result in low numbers of small mammals in young stands. Limitations could be especially severe during winter when truffle biomass and other foods are at seasonal lows (North et al. 1997). We hypothesize that this diversity of food sources underlies the structure and abundance of forest-floor small-mammal communities and that neither management by thinnings nor management with legacies provided that diversity of food sources.

Of three species primarily responsible for the differences between small-mammal communities in legacy and thinned stands, two had niches strongly associated with understory vegetation (creeping vole and deer mouse, Carey and Johnson



legacies and forest managed with thinning, Puget Trough, Washington. Taxa are identified by alpha codes comprised of first 2 *P. oreas, Sorex monticolus, S. trowbridgii, S. vagrans.*

1995), and one with the soil-layer litter (montane shrew, Hawes 1977). Thinned stands had greater shrub volumes and herbaceous cover than legacy stands. No forest-floor small-mammal species achieved significantly greater abundance under legacy management, an unexpected result that suggests (1) that statistical correlations between shrew-moles and coarse woody debris (Carey and Johnson 1995) do not represent a direct cause and effect relationship and (2) a second hypothesis that there may be some substitutability in providing protective cover and organic inputs to the forest floor between dense low understory vegetation and coarse woody debris. Furthermore, stumps and logs in legacy stands may have been unable to attain their full potential as habitat elements because of poor understory development—covers of both coarse woody debris and understory vegetation were low compared to old-growth forests. Carey and Johnson (1995) found that abundances of most small mammals were correlated with both understory vegetation and coarse woody debris. The distribution of patches of dense understory vegetation was more important than mean abundance and that mammal species responded differently to different kinds of vegetation. Carey et al. (1999*a*) hypothesized that a synergistic response of small mammals occurs when a diversity of vegetation site-types (discrete repeatable associations that differ in composition and structure) in the understory and coarse woody debris are arrayed in close juxtaposition in a fine-scale mosaic. This synergy is due, in part, to pre-interactive

TABLE 5. Distribution of small mammal biomass in four 4-ha sampling plots in each of 2 forest tracts on Fort Lewis, Washington, 1992-1994; forest managed with retention of legacies[1] (L) or managed with intensive thinning (T).

Species	Mnka[2] Forest	Mean Body Mass (g) $\bar{x}$	(se)	Mean Stand Biomass (g) $\bar{x}$	(se)	$\bar{x}$	(se)	P
Clethrionomys gapperi	L	22.2	(3.2)	15.8	(0.2)	351	(50)	0.377
	T	26.4	(4.0)	15.8	(0.3)	417	(65)	
Microtus oregoni	L	4.3	(1.5)	14.4	(1.4)	61	(22)	0.000
	T	33.9	(5.4)	14.3	(0.3)	485	(75)	
Peromyscus maniculatus	L	9.2	(2.5)	14.4	(0.7)	133	(32)	0.001
	T	25.7	(4.0)	14.5	(0.3)	373	(56)	
Sorex trowbridgii	L	53.3	(3.4)	4.4	(0.0)	235	(15)	0.427
	T	49.7	(3.4)	4.4	(0.0)	219	(14)	
Sorex monticolus	L	31.3	(2.5)	5.6	(0.1)	175	(15)	0.008
	T	46.4	(4.1)	5.7	(0.1)	265	(26)	
Neurotrichus gibbsii	L	16.8	(2.5)	7.2	(0.1)	121	(19)	0.802
	T	14.8	(3.3)	7.7	(0.1)	114	(25)	
Sorex vagrans	L	4.8	(1.2)	3.7	(0.1)	18	(5)	0.177
	T	2.6	(0.9)	4.0	(0.1)	10	(4)	
Peromyscus oreas	L	0.5	(0.3)	14.6	(2.8)	7	(7)	0.406
	T	1.0	(0.5)	17.7	(8.5)	18	(9)	
Mean stand biomass	L	...	...	...	...	1101	(14)	0.000
	T	...	...	...	...	1901	(23)	
Mean biomass / hectare	L	...	...	...	...	275		
	T	...	...	...	...	475		

[1] Logs, snags, and residual trees from the previous stand.

[2] Minimum number known alive.

[3] Significance of Mann-Whitney U tests for differences between species man biomass between management treatments L and T.

niche diversification that promotes high abundances and diversity in the forest-floor small mammal community. Our results support this third hypothesis. Contrary to observed patterns of forest-floor small mammals, flying squirrels were more abundant in legacy stands; this result was confirmed by sampling aimed specifically at squirrels, as was the greater abundance of chipmunks in thinned stands (Carey 2000).

Species Responses to Management Strategies

Four common species—Trowbridge's shrew, vagrant shrew, shrew-mole, and red-backed vole–were equally abundant under the two management strategies. Critical niche dimensions for these species may be more directly tied to biological activity at the soil-litter interface than to either understory vegetation or woody legacies in the forest environment. Montane shrews were more abundant in thinned stands than legacy stands and in old growth more than second growth on the Olympic Peninsula. Montane shrews forage for invertebrates within unconsolidated soil organic layers (Terry 1974) and prefer *mor* humus (organic litter distinct from mineral soil) over *moder* humus (netlike structure of organic and mineral particles) (Hawes 1977). High shrub volume and deciduous litter in the thinned sites could have enhanced *mor* humus development and fostered greater invertebrate diversity and abundance thus benefiting montane shrews. We did not measure

	S. Washington Cascades[1]		Olympic Peninsula[2]		Puget Trough[3] young stands	
	Old growth	Young	Old growth	Young	Thinned	Legacies
Rank	CPU	CPU	CPU	CPU	CPU	CPU
1	1.1 SOTR	1.0 SOTR	8.0 SOTR	5.2 SOTR	3.5 SOTR	3.6 SOTR
2	1.0 CLGA	1.0 SOMO	5.4 PEOR	2.6 CLGA	3.3 SOMO	2.1 SOMO
3	0.8 SOMO	0.7 CLGA	5.2 SOMO	2.4 PEOR	2.4 MIOR	1.5 CLGA
4	0.7 PEOR	0.4 PEOR	2.8 CLGA	2.3 SOMO	1.9 CLGA	1.1 NEGI
5	0.3 PEMA	0.2 SOVA	1.3 NEGI	1.2 MIOR	1.8 PEMA	0.6 PEMA
6	0.2 NEGI	0.1 NEGI	0.9 MIOR	0.9 NEGI	1.1 NEGI	0.3 SOVA
7	0.1 MIOR	0.1 PEMA	0.6 PEMA	0.5 PEMA	0.2 SOVA	0.3 MIOR
8	0.1 SOVA	0.1 MIOR	0.5 SOVA	0.5 SOVA	0.1 PEOR	0.03 PEOR
Total CPU	4.3	3.6	24.7	15.6	14.3	9.53

[1] Four night snap-trap session combined with 30-34 night pitfall-trap session per year.

[2] Four night snap-trap session per year.

[3] Eight night live-trap session per year.

Figure 2. Small mammal community structures listed from most to least abundant species for the southern Washington Cascade Range, 1984-1985 (West 1991); the Olympic Peninsula, Washington, 1987-1989 (Carey and Johnson 1995); and the Puget Trough, Washington, 1992-1994. Lines connect species with significantly different abundances between stand types within a region ($P \leq 0.05$). Note low numerical importance of *P. oreas* in Puget Trough communities. Taxa are identified by alpha code comprised of first 2 letters of genus and species: *Clethrionomys gapperi, Microtus oregoni, Neurotrichus gibbsii, Peromyscus maniculatus, P. oreas, Sorex monticolus, S. trowbridgii, S. vagrans.*

depth, successional stage, or quality of organic litter (Shaw et al. 1991) under our two management strategies, but understanding litter layers might be key to understanding patterns of abundance of small mammals. Our fourth hypothesis is that the soil-litter interface is a key element in structuring small-mammal communities.

Coarse woody debris cover was significantly lower in thinned stands than in legacy stands and very low in abundance compared to natural stands (West 1991, Carey and Johnson 1995). However, the 1-2% cover of coarse debris in thinned stands represented a minimum 400 m^2 of coarse woody debris per stand. In a companion telemetry study (S. Wilson, unpublished data) of deer mice, Columbian mice, and red-backed voles, nearly all individuals in thinned stands used stumps and logs as denning or resting sites. It appears that stumps and logs, even in low densities, are an important resource for small mammals and the value of these legacies to small mammals may be bolstered by understory vegetation. Our fifth hypothesis is that the fungal and invertebrate activity supported by downed wood (Harmon et al. 1986), and its protective cover (Hayes and Cross 1987), may help to maintain minimum carrying capacities in stands managed with legacies for those small mammals not directly reliant on herbs, shrubs, or invertebrates associated with understory plants (Tallmon and Mills 1994, Carey and Johnson 1995).

Columbian mice were rare. This mouse has been related to diverse understories, midstories including shade-tolerant trees, coarse woody debris, and tall canopies (Dalquest 1948, West 1991, Carey and Johnson 1995)—but the determinants of Columbian mouse abundance remain unknown. Certainly there is a greater overall abundance and variety of seeds, fruits, and nuts in forests with complex canopies. Deer mice for example, are known to consume fruits, seeds, and invertebrates (Van Horne 1982, Gunther et al. 1983) and montane shrews are known to consume conifer seed (Gunther et al. 1983). Greater shrub prevalence

(Carey and Johnson 1995) plus greater canopy tree species richness producing more abundant and varied conifer seed may account for greater abundances of a number of species in old growth. Our study sites had monospecific canopies without midstories; legacy sites had sparse to moderate understories. Thus, low abundances of the habitat-generalist deer mouse (Baker 1968) in legacy stands was not surprising. In a companion study (S. Wilson, unpublished data), we found fluorescent pigment trails (Lemen and Freeman 1985) on the forest floor and in branches of fruiting salal suggesting that deer mice were able to exploit the additional resources provided by the greater shrub volume in thinned stands. The relative abundances of deer mice in our thinned stands were large compared to small-mammal communities in other regions. Deer mice may replace Columbian mice as the dominant forest mouse in rapidly changing, simply structured, early seral environments (Songer et al. 1997). However, low abundances of Columbian mice in young forests on the Olympic Peninsula and the southern Washington Cascades were not accompanied by a reciprocal increase in deer mice (West 1991; Carey and Johnson 1995).

Vagrant shrews were very low in abundance on our study sites–but were low in abundance elsewhere as well (Carey and Johnson 1995). Low abundances of creeping voles in legacy stands is easily explained by low amounts of herbaceous vegetation there (Carey and Johnson 1995). Creeping voles reach peak densities in clearcuts and old fields (Dalquest 1948, Hooven 1973). High relative abundances of creeping voles on thinned sites were probably due to lingering effects of disturbance on the understory—numerous weedy species were abundant in thinned stands but rare or absent from legacy stands (Carey et al. 1999*b*, Thysell and Carey 2000).

Implications

Repeated thinning fostered development of understory vegetation on our sites and in forests of similar age and management history in western Oregon (Bailey and Tappeiner 1998). Because understory vegetation is 1) responsive to management and 2) seemed to have a large influence on *Peromyscus* and *Microtus* abundance, thinning has potential to remedy low small-mammal abundance in young managed forest. Conventional thinnings result in systematically spaced trees and dense low understories dominated by a few native plants; development of shade-tolerant regeneration may be precluded; and vegetation-site type diversity reduced (Thysell and Carey 2000). Variable-density thinning (Carey 1995; Carey and Curtis 1996; Carey et al. 1999*a*,*b*) manipulates spatial heterogeneity in the canopy to produce diverse understories. Combining vegetation management with management of decadence, including retention of woody legacies (Carey et al. 1996*b*; Carey et al. 1997; Carey et al. 1999*a*) could provide markedly greater benefits than either strategy we examined here.

Without intentional management of forest processes, including decadence (Carey 1999*a*), timber harvesting can lead to a decline in legacies, simplification of stand structure, and lowered habitat quality with consequences for trophic webs (Spies and Cline 1988; Halpern and Spies 1995; Carey and Curtis 1996; Harmon et al. 1996; Carey et al. 1999*a*; Carey et al. 1999*b*). Future tests of small mammals should consider the effects of stand structure and canopy heterogeneity on forest floor processes.

Limitations

It is possible that population density may be a misleading indicator of habitat quality (Van Horne 1983), but our demographic data did not indicate that was the case in our study. Population structures for most species were similar under each management strategy and we believe that abundance was an appropriate indicator of small-mammal habitat quality.

Temporal variation in species abundances can confound or obscure effects of treatment and comparisons among studies. We observed a simultaneous increase in the abundances of five species between 1993 and 1994. Only deer mice showed an interactive effect between year and management strategy. One or more extraneous factors, such as weather, conifer seedfall (Gashwiler 1979; Sullivan 1979; Gunther et al. 1983), or invertebrate outbreak (Elkinton et al. 1996) appeared to affect animal abundance across the entire study area. Unfortunately, we cannot identify the cause.

But, given our three years of data from four sampling units per management strategy, and given parallels with other retrospective studies, we have confidence in our findings as they apply to our study areas and in general to second-growth Douglas-fir forests. Our sites did not include the full range of habitat variability in western Washington forests and our results should be applied cautiously to other forests of different location, age, and composition. Our ability to detect a continuous response to legacies and understory vegetation was constrained because we tested only two levels of each. We observed small-mammal communities only during summer, and our results may not hold for other seasons.

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Site Index Conversion Equations for Western Redcedar and Western Hemlock

Abstract

Equations that predict site index for western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) from the site index of western redcedar (*Thuja plicata* Donn ex D. Don) (or vice versa) are needed to make good forest management decisions in the Pacific North West. Site index data for hemlock and redcedar were collected from sample plots located in two major ecological subzones in southern coastal British Columbia. Geometric mean regression was used to estimate the parameters of a linear model relating the site indices of hemlock and redcedar. The correlation between the site indices was high, indicating a good fit to the linear model. In general, the site index of hemlock is higher than the site index of redcedar, indicating that hemlock is more productive than redcedar on a given site. A validation procedure showed that one set of conversion equations was adequate for both ecological subzones. The conversion equations can be applied in mixed species stands or in stand conversion situations, although caution is required for both applications.

Introduction

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don) commonly grow in mixtures on the coast of northwestern North America. There are many similarities between these species (Burns and Honkala 1990). Their ranges extend from California to Alaska on the coast, and both species also grow in interior British Columbia, Washington, Idaho, and Montana. Redcedar and hemlock are very shade tolerant and both are considered to be late succession species. As their ranges are quite similar, their sites have similar climatic and edaphic characteristics, although redcedar can grow on drier sites than hemlock. When grown in mixed stands, hemlock will usually overtop redcedar.

Western redcedar and western hemlock are often found in mixed stands, making growth and yield information on redcedar and hemlock mixtures important. Site index, which in British Columbia is top height at breast height age 50, is a particularly important piece of information because it is a measure of site quality. Site index is used along with stand density to estimate volume yields. Therefore, site index estimates for both species are required to estimate their yields when they both occupy the same site.

Site index may not be estimable for both species when redcedar and hemlock are growing in a mixed stand. This would be the case when height and age data are missing for one species, or if the trees of one species have some early suppression or are not in the dominant or upper co-dominant layer. Situations may also arise where a stand is harvested and a different species lacking site index data is regenerated on the site. In these cases, site index conversion equations may be used to estimate the site index of one species from the site index of another species (Carmean 1972, Hägglund 1981, Nigh 1995).

This paper describes the development of site index conversion equations for western redcedar and western hemlock on the southern coast of British Columbia.

Study Area

The study area was comprised of two subzones in the Coastal Western Hemlock (CWH) biogeoclimatic zone in British Columbia (Meidinger and Pojar 1991). The study plots were located north and east of Vancouver, B.C., in two variations of the CWH zone: the dry maritime (dm) subzone and in the submontane very wet maritime subzone (vm1) (Green and Klinka 1994).

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The dm subzone has relatively dry summers, whereas the vm1 subzone has relatively wet cool summers. The dm subzone has a similar climate to the *Pseudotsuga menziesii–Tsuga heterophylla* forest, and the vm1 subzone to the *Picea sitchensis–Tsuga heterophylla* forest as delineated by Franklin and Dyrness (1973) for Washington and Oregon.

Methods

Study Plots

Sixty-three 0.04 ha plots were established in stands with both western hemlock and western redcedar trees. Nineteen of the 63 plots were located in the dm subzone and 44 plots were in the vm1 subzone. The samples were established in stands that had been logged and burned in the early 1900s. The emerging natural regeneration after burning contained extensive areas of even-aged western redcedar stands with minor components of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) and western hemlock.

Within each study plot, five dominant trees of each species were selected as the sample trees. The height and breast height age of the sample trees were measured and recorded. The heights and ages were averaged and the height-age models for western redcedar and western hemlock (Nussbaum 1996) were used to estimate site index. This resulted in site index pairs for the 63 plots.

Data Analyses

In a preliminary analysis, the site indices of western hemlock were plotted against the site indices of western redcedar. This graphical analysis suggested that a linear model relating the site indices of the two species was appropriate, where:

$$SI_{Hw} = m \times SI_{Cw} + b + \varepsilon, \text{ or} \quad (1)$$

$$SI_{Cw} = m \times SI_{Hw} + b + \varepsilon, \quad (2)$$

SI_{Hw} is the site index at breast height age 50 for western hemlock, SI_{Cw} is the site index at breast height age 50 for western redcedar, m is the slope parameter, b is the intercept parameter, and ε is an error term.

The parameters, m and b, of the site index conversion equation were estimated using geometric mean regression (Leduc 1987, Nigh 1995, Ricker 1973, 1984). This method was chosen because we required a system of two invertible linear regression models, that is, two models whereby one regression model can be produced from the other by mathematically inverting it.

The parameters of the geometric mean regression line, m and b, were estimated from the following equations (Leduc 1987, Nigh 1995), where:

$$\hat{m} = \text{sgn}(r) \times \frac{S_Y}{S_X}, \quad (3)$$

$$\hat{b} = \overline{Y} - \hat{m} \times \overline{X} \quad (4)$$

$\hat{m}$ and $\hat{b}$ are estimates of m and b, respectively, r is the correlation coefficient for the site index pairs, sgn(r) is: +1 if r is positive, -1 if r is negative, and 0 if r is 0, S_Y and S_X are the standard deviations of the dependent and independent variables, respectively, and $\overline{Y}$ and $\overline{X}$ are the means of the dependent and independent variables, respectively. For model (1), $Y = SI_{Hw}$ and $X = SI_{Cw}$, and for model (2), $Y = SI_{Cw}$ and $X = SI_{Hw}$. Note that the parameters of models (1) and (2) can be estimated from the data or the parameters can be estimated for one model and derived by algebraic manipulation for the other model. Both methods give the same results.

Formulae for the 95% confidence intervals for the geometric mean regression parameters, $\hat{m}$ and $\hat{b}$, are given in equations (5) and (6) (Leduc 1987 [but note the errors in equations [10] and [11] in this article], Rayner 1985), respectively,

$$\left[\hat{m} \times \sqrt{\frac{1-Q}{1+Q}}, \hat{m} \times \sqrt{\frac{1+Q}{1-Q}}\right], \text{ and} \quad (5)$$

$$\left[\hat{b} - t_{n-2,0.975} \times \sqrt{\frac{S_{YY}}{n} \times (1-r) \times \left(2 + \overline{X}^2 \times \frac{1+r}{S_{XX}}\right)}, \right.$$
$$\left. \hat{b} + t_{n-2,0.975} \times \sqrt{\frac{S_{YY}}{n} \times (1-r) \times \left(2 + \overline{X}^2 \times \frac{1+r}{S_{XX}}\right)}\right], \quad (6)$$

where $t_{n-2,0.975}$ is the 0.975^{th} quantile of the Student's t distribution with n-2 degrees of freedom, n is the number of observations, S_{YY} and S_{XX} are the variances of the dependent and independent variables, respectively, and

$$Q = t_{n-2,0.975} \sqrt{\frac{1-r^2}{r^2 \times (n-2)}}. \quad (7)$$

Models (1) and (2) were fit to the whole data set (the combined models) and to the data for the dm and vm1 subzones individually (the dm and vm1 models). Cross-validation was done to

TABLE 1. Results of the geometric mean regression analysis.

Data set	Model		Parameter Estimate	95% confidence interval Lower bound	Upper bound	r
Combined	$SI_{Hw} = m \times SI_{Cw} + b$	m̂	1.048	0.8441	1.301	0.82
		b̂	1.256	-3.502	6.014	
	$SI_{Cw} = m \times SI_{Hw} + b$	m̂	0.9545	0.7688	1.185	
		b̂	-1.199	-5.944	3.546	
dm	$SI_{Hw} = m \times SI_{Cw} + b$	m̂	0.8437	0.6549	1.087	0.90
		b̂	7.478	2.597	12.36	
	$SI_{Cw} = m \times SI_{Hw} + b$	m̂	1.185	0.9198	1.527	
		b̂	-8.864	-16.50	-1.229	
vm1	$SI_{Hw} = m \times SI_{Cw} + b$	m̂	1.164	0.9065	1.495	0.79
		b̂	-2.074	-7.790	3.642	
	$SI_{Cw} = m \times SI_{Hw} + b$	m̂	0.8588	0.6688	1.103	
		b̂	1.782	-2.795	6.369	

determine if the combined model was adequate or if we require a separate model for the dm and vm1 subzones. Each observation was sequentially removed from a dataset, models (1) and (2) were re-fit, and the error in the estimated cedar and hemlock site index was calculated for the removed observation. The errors were tested for normality with the W test (Shapiro and Wilk 1965) and for bias with a t-test. The F_{max} statistic (Hartley 1950, Neter et al. 1990) was used to test whether the dm and vm1 models resulted in a significantly different variance in the errors in estimated site index for the dm and vm1 data.

Results

Table 1 shows the results of the geometric mean regression for models (1) and (2) fit to the combined, dm, and vm1 data. The mathematical equivalence of the fitted models (1) and (2) can be easily demonstrated by inverting one model and noticing that the parameters are the same (with tolerance for rounding errors) as the parameters in the complementary model.

Figures 1 and 2 are plots of the data points overlaid on the combined and dm/vm1 models, respectively. These figures show a strong relationship between the site indices of western redcedar and western hemlock when they are growing in a mixed stand. This observation is verified by the high correlation coefficients (Table 1).

The results of the model testing are given in Table 2. The W statistic indicates that the errors in estimated site index are normally distributed. This result is important because the t-test for bias and the F_{max} test both assume that the data are normally distributed. The t-tests show that all models are unbiased, that is, the mean errors from the models are not statistically significantly different from zero. The critical value for the F_{max} test at a significance level of a = 0.05 is approximately 2.62 and 1.90 for two populations with 18 and 43 degrees of freedom, respectively. For

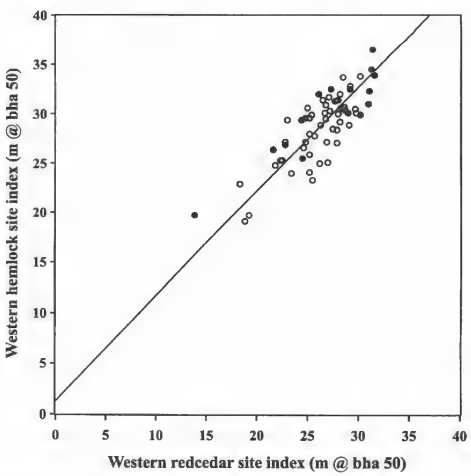

Figure 1. Western hemlock and western redcedar site indices from the dm subzone (•) and vm1 subzone (○) with the fitted geometric mean regression line (————) estimated from all the data.

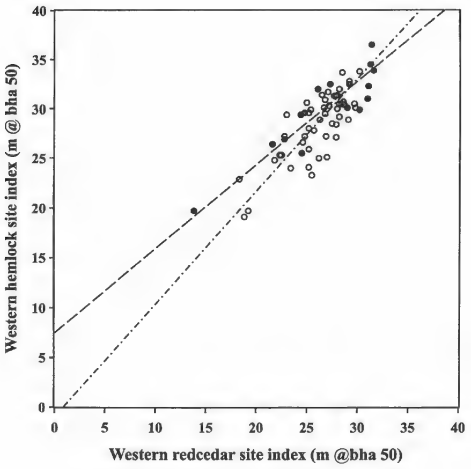

Figure 2. Western hemlock and western redcedar site indices from the dm subzone (•) and vm1 subzone (○) with the fitted geometric mean regression line estimated from the dm subzone data (– – –) and from the vm1 subzone data (– · –).

the cedar data, F_{max} = 1.10 (4.84÷4.39) and 1.11 (4.27÷3.83) for the dm and vm1 subzones, respectively. For the hemlock data, F_{max} = 1.46 (4.98÷3.40) and 1.12 (5.21÷4.66) for the dm and vm1 subzones, respectively. These results indicate that the variances of the errors from the combined and the dm/vm1 models are not significantly different. We conclude from the t-test and the F_{max} tests that the combined model is not biased, nor does it have poorer precision when compared to the dm and vm1 models, and therefore is adequate for both subzones.

Discussion

This study clearly shows that the site index of western redcedar can be estimated from the site index of western hemlock, and vice versa, with the following models:

$$SI_{Hw} = 1.048 \times SI_{Cw} + 1.256, \text{ and} \quad (8)$$

$$SI_{Cw} = 0.9545 \times SI_{Hw} - 1.199. \quad (9)$$

Site index conversion equations (8) and (9), developed with data from both the dm and vm1 subzones, are adequate for both subzones. The equations are applied by obtaining the site index for either western hemlock or western redcedar. The known site index is then input into either equation (8) or (9), depending on whether the site index of redcedar or hemlock is known, to estimate the site index of the complementary species. The conversion equations are designed specifically for mixed species stands. However, they can also be used for stand conversion situations, that is, when a stand of one species is harvested and regenerated with another species. In this situation, species interactions will not be present so the estimated site index may be biased.

The use of the conversion equations is contingent on the availability of an unbiased site index estimate for one of the species in the stand. This site index can be obtained from trees whose height growth has not been impeded by non-site factors, such as suppression or disease, or from some other method such as soil-site relationships. If a biased site index is used in the model, then the converted site index will be biased as well. Even when a good site index estimate is available, the conversion equations must be applied judiciously. For example, the species for which a site index is being

TABLE 2. Results of the model testing. The dm and vm1 datasets have 19 and 44 observations, respectively. The p-values for the t-test and W statistic are in brackets.

		Western redcedar error				Western hemlock error			
Model	Dataset	Mean	Variance	t-test	W	Mean	Variance	t-test	W
Combined	dm	-0.719	4.39	-1.50	0.959	0.763	4.98	1.49	0.963
				(0.152)	(0.553)			(0.153)	(0.629)
	vm1	0.303	4.27	0.971	0.977	-0.309	4.66	-0.951	0.977
				(0.337)	(0.651)			(0.347)	(0.650)
dm	dm	-0.0547	4.84	-0.108	0.949	0.0374	3.40	0.0884	0.944
				(0.915)	(0.382)			(0.931)	(0.319)
vm1	vm1	-0.00295	3.83	-0.0100	0.981	0.0100	5.21	0.0290	0.980
				(0.992)	(0.783)			(0.977)	(0.750)

estimated may not attain the potential height implied by the site index because of, for example, suppression. Practitioners should also be aware that there is an error associated with the site index estimate from any conversion equation. Therefore, the precision of the site index estimate is degraded when conversion equations are applied sequentially. This may be the case when a site index conversion from species A to C is desired but a conversion equation is not available. Therefore, a practitioner may have to convert the site index of species A to B, then from species B to C, but the cost will be reduced precision.

The site index of the western hemlock was consistently higher than the site index of the western redcedar. This is in agreement with previous observations that indicate that redcedar is often overtopped by hemlock when grown in mixed stands (Burns and Honkala 1990). This result also demonstrates that site index is a species specific concept. Even though the two species are growing on the same site, they do not grow at the same rate and hence do not have the same productivity on a given site.

Conclusion

This study makes site index conversion equations accessible for western hemlock and western redcedar. These conversion equations will be important in good forest management because hemlock and redcedar are common species on the coast of northwestern North America. The data for the equations were collected from two major ecological subzones, and one conversion equations is adequate for both subzones.

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Influence of Partial Harvesting on Stream Temperatures, Chemistry, and Turbidity in Forests on the Western Olympic Peninsula, Washington

Abstract

Stream temperatures, chemistry and turbidity were monitored in two partially harvested (7–33%) watersheds, Rock and Tower creeks, and an uncut old-growth watershed, West Twin Creek in the Hoh River Valley on the Olympic Peninsula, Washington. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) was replanted in the harvested areas and red alder (*Alnus rubra* Bong.), a nitrogen fixer, dominated the riparian areas in the sampling sites on Rock and Tower creeks. We collected grab stream water samples monthly, from May 1996 to June 1998 and analyzed them for pH, electrical conductivity, total N and P, and major cations and anions. Stream temperatures were monitored continuously and turbidity was monitored monthly from May 1997 to June 1998. Partial harvesting had little influence on stream temperature, chemistry and turbidity 11–15 years after harvesting. Stream temperatures were more seasonally variable in the harvested streams compared to the unharvested old-growth site with an average summertime maximum elevated by 3.5°C. Maximum stream temperatures did not exceed 16°C in any stream and therefore salmonid species are not likely to be affected. There were significant differences in concentrations of some cations, anions and EC between the old-growth and the partially harvested watershed streams, but in most cases concentrations were actually higher in the unharvested watershed. Nitrate concentrations and stream turbidity were not significantly higher in the harvested watersheds.

Introduction

Forest management practices can alter the temperature, turbidity, and chemistry, of streams (Beschta and Taylor 1988, Binkley and Brown 1993). For example, removal of streamside vegetation increases the amount of solar radiation reaching the stream and elevates temperatures, which may be slow to recover even with regrowth of vegetation (Hostetler 1991). Although increased solar radiation may result in an increase in stream productivity, increases in temperature may negatively affect temperature sensitive species, particularly salmon (McCullough 1999). Harvesting can also result in increased siltation and stream turbidity (Binkley and Brown 1993) which may deplete salmon habitat. In addition, forest removal can result in increases of stream nitrate levels due to increased soil nitrification, although concentrations generally stay below drinking water standards (Binkley and Brown 1993). Recently, partial harvesting, has become a component of ecosystem management (Franklin 1992). Therefore, it is important to investigate the influence of partial harvesting on key environmental variables that affect stream health.

In the Pacific Northwest disturbed riparian areas are generally recolonized by red alder (*Alnus rubra* Bong.), a deciduous tree with a symbiotic bacteria in root nodules capable of fixing nitrogen. Wigington et al. (1998) hypothesized that the variability of nitrate concentrations and other chemical constituents found in 48 coastal Oregon streams was directly related to the red alder vegetation. However, the regrowth of red alder along the stream channel does not immediately result in increased nitrogen inputs to a stream, since it takes time for nitrogen-fixing bacteria to establish (Van Miegroet et al. 1992). It is important to determine if the legacy of forest harvest in the Pacific Northwest has resulted in shifts in stream chemistry, turbidity and temperature that negatively influence stream health.

Although the influence of harvesting on Pacific Northwest streams has been studied (Feller and Kimmins 1984, Beschta and Taylor 1988, Binkley and Brown 1993), few studies reporting changes in stream temperature, nitrate concentrations and turbidity after harvesting have been conducted in coastal streams, particularly on the western Olympic Peninsula of Washington. Some studies have been conducted in coastal Oregon (Miller and Newton 1983). We have been studying stream chemistry in a small old-growth forested watershed in the Hoh River valley (West

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Twin Creek) for more than 15 years (Edmonds et al. 1998) and in 1996 we initiated a study to compare data from this watershed with data from two adjacent partially harvested watersheds, Rock and Tower creeks, where the riparian zones are now dominated by red alder. The chemistry of these streams was monitored before harvesting (Larson 1979). Our objective was to determine if there were differences in stream temperature, chemistry and turbidity in the two partially harvested watersheds relative to the adjacent pristine old-growth watershed 10–15 years after harvesting.

Study Sites

West Twin Creek Watershed

The 58 ha West Twin Creek watershed is located in the Hoh River Valley on the western side of Olympic National Park (Figure 1), approximately 32 km inland from the ocean, and is described in detail in Edmonds et al. (1998). West Twin Creek is a first order stream. Stream width varies from 1–2 m and the average channel slope is 25.6 percent (Table 1). Elevations in the watershed range from 240 to 800 m, sampling was done at 240 m, just above the weir. Mean January and July air temperatures are 4 and 16°C, respectively at the Hoh Ranger Station. Soil temperatures never fall below 0°C and rarely exceed 20°C. Annual rainfall averaged 3333 mm from 1985 to 1994 and is strongly seasonal with most falling from October to May (Edmonds et al. 1998). Snow rarely falls in the lower elevations, but a weak snowpack may develop above 600 m. Annual discharge from the watershed from 1985 to 1994 ranged from 54 to 89% of precipitation. Soils are

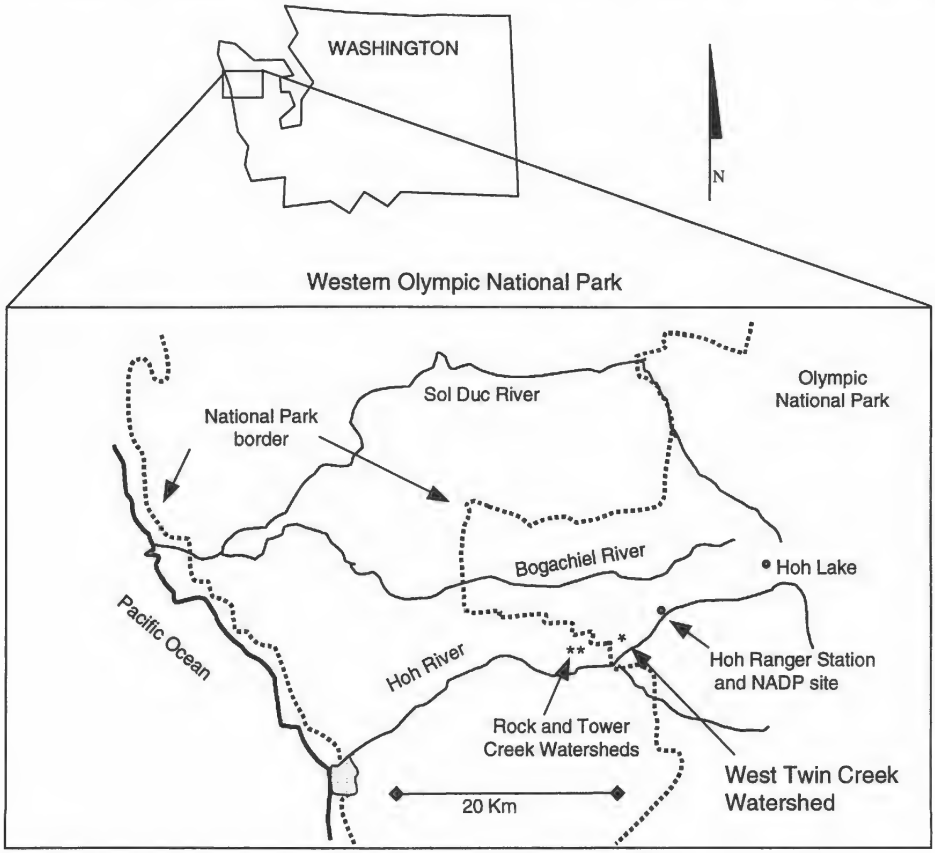

Figure 1. Location of the West Twin, Rock and Tower Creek watersheds in western Olympic National Park, Washington.

inceptisols, and forest floor depth ranges from 5 to 10 cm (Edmonds et al. 1998). The watershed encompasses two vegetation zones identified by Franklin and Dyrness (1973). The lower watershed is in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone, while the upper watershed is in the Pacific silver fir (*Abies amabilis* (Dougl.) Forb.) zone. The main tree species in the watershed are Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock, western red cedar (*Thuja plicata* Don.) and Pacific silver fir. The forest is uneven-aged with oldest trees more than 600 years.

Rock and Tower Creeks

Rock (235 ha) and Tower (263 ha) Creek watersheds are located on Washington State Department of Natural Resources lands just outside of the Olympic National Park (Figure 1) and are 24 and 26 km inland from the ocean. Both streams are slightly wider than West Twin Creek (3–4 m) at the sampling sites just above the weirs, and are higher order streams. However, all 3 watersheds extended over similar elevations, with the Rock and Tower watersheds ranging from 170 to 825 m and from 230 to 900 m, respectively (Table 1) from the weirs to the upper boundaries. Average channel slopes are 21.7 and 21.3 percent for Rock and Tower creeks, respectively. All sampling was done at the lower limit of the elevation range just above the weirs. The climate in the watersheds is similar to that in the West Twin Creek watershed and annual discharge from 1975 through 1977 ranged from 86 to 91% of precipitation (Larson 1979). Soils are inceptisols (Larson 1979).

Both watersheds originally contained old-growth forest similar to that in the West Twin Creek watershed (Larson 1979). In 1981, a small portion, 7%, of the Rock Creek watershed was logged while 33% of Tower Creek watershed was logged from 1985 to 1987. Logging did extend to the stream channel, including the area adjacent to our stream sampling. Both sites were replanted with Douglas-fir and there is natural regeneration of western hemlock. Red alder dominates the riparian zones. Anadromous fish are not present above the weirs in any of the watersheds.

Methods

Stream temperatures

Stream temperatures were monitored using Optic Stowaway® temperature dataloggers starting on 25 June 1996 in Rock and Tower creeks, and on 10 July 1996 in West Twin Creek. Monitoring continued through 15 June 1998. Daily maximum, minimum and average temperatures were determined.

Stream chemistry

Concentrations of cations, anions, and total N and P, Electrical Conductivity (EC), and pH were determined from grab samples collected from the three creeks once every four weeks from 15 May 1996 through 4 June 1998. Samples were placed in a cooler for transportation back to the laboratory, and analyzed at the Analytical Services Laboratory at the College of Forest Resources, University of Washington. Electrical conductivity, pH and alkalinity (reported as HCO_3) were determined on unfiltered samples. EC was determined with a YSI Model 31 Conductivity Bridge (Yellow Springs Instrument Co., Yellow Springs, OH 45387) and corrected to 25°C. pH was determined with a Radiometer PHM85 pH meter (Radiometer, Copenhagen, Denmark). Alkalinity was determined by titration to an end point of pH 5.

TABLE 1. Watershed characteristics.

Watershed	% Harvested	Elevation Gradient (m)	Average Channel Slope, S_c (%)[1]	Catchment Length (km)	Aspect (degrees)	Distance from Ocean (km)
Rock	7	170-825	21.7	2.5	200	24
Tower	33	230-900	21.3	2.2	215	26
West Twin	0	200-800	25.6	0.9	145	32

[1] S_c=(elevation at source - elevation at mouth)/stream length (values were estimated from USGS topographic map, scale 1:64,000 enlarged by 400%).

Remaining sample material was filtered through Whatman GF/A filters and stored at 4°C and analyzed within a month after arrival at the lab.

Solutions were analyzed for Ca, Mg, K, and Na, using Inductively Coupled Plasma atomic emission spectrometry. Ammonium was determined with a Technicon Autoanalyzer II (Technicon, Tarrytown, NY 10591). Sulfate, Cl, NO_3 and PO_4 were determined with a Dionex 2100 Ion Chromatograph (AS4A and AG4A columns) (Dionex, Sunnyvale, CA 94088). Macro Kjeldahl digests were done on all samples having sufficient volume and those digests were analyzed for total N and P using a Technicon Autoanalyzer II.

Turbidity

Turbidity in the three creeks was determined using a HF Scientific, Inc. Model DRT-15CE portable turbidity meter. Samples were taken every four weeks from May 1997 to June 1998 at the same time that samples were taken for stream chemistry. Turbidity was recorded in nephelometric turbidity units (NTUs). Except for the samples taken on 17 December 1997 and on 14 January 1998 stream samples were taken in midstream and turbidity recorded after approximately 40–60 seconds. On 17 December 1997 and 14 January 1998 three samples were taken across the stream and turbidity was read after 30, 35 and 40 seconds and the average was calculated.

Statistical analyses

Differences in average concentrations of elements and turbidity in the three streams were detected using one-way ANOVA with a Post Hoc Tukey HSD test ($p= 0.05$), using SPSS® software.

Results and Discussion

Stream temperatures

Daily average and maximum temperatures for the three streams over the period from 15 May 1996 to 15 June 1998 are shown in Figures 2A and 2B, respectively. Some data are missing in summer 1997 because the data loggers malfunctioned in Rock and Tower creeks. Daily average temperatures in West Twin Creek were lower in summer and higher in winter than those in Rock and Tower creeks (Figure 2A). Rock and Tower creeks were similar. The range was less variable in West Twin Creek (5.4–11.4°C) than in Rock and Tower creeks (1.9–15.1°C).

Daily maximum stream temperatures (Figure 2B) had similar patterns to the average stream temperatures with greater seasonal fluctuations in Rock and Tower creeks than West Twin Creek. Maximum temperatures in the summer were higher in Rock and Tower creeks (15.4°C) than West Twin Creek (12.1°C) and lower in winter (3.7 and 6.0°C, respectively). Minimum temperatures were also more extreme in harvested watershed creeks with the lowest minimum temperature in Rock Creek, 1.2°C compared to 5.5°C in West Twin Creek.

Higher stream temperatures and greater fluctuations in Rock and Tower creeks compared to West Twin Creek could be due to harvesting activities. In Oregon, Hall and Fredriksen (1988) found summer daily average stream temperatures to be 2.5 to 3°C higher in watersheds with 25 percent harvested area than control watershed streams. With 66 percent overstory removal in British Columbia, Feller (1981) found a 5°C increase in summer average daily stream temperatures. These increases are similar to the increases we found in summer (Figure 2A). In Salmon Creek watershed, Oregon, Beschta and Taylor (1988) found increased maximum and minimum stream temperatures over a 30-year period due to the cumulative effects of forest harvesting. This included disturbance of regrowing streamside vegetation during peak flow events which prolonged recovery of riparian shade. In another Oregon watershed, Streamboat basin, extensive logging has been conducted since 1955, which did not include leaving riparian buffer strips until the early 1970s (Hostetler 1991). Stream temperatures have only gradually recovered in the basin and summer high temperatures remained near the upper tolerance level for steelhead in some streams (Hostetler 1991). In our study, the maximum temperatures were not above water quality standards, however, some differences were observed 11–15 years after harvest. Rock and Tower creeks are larger creeks than West Twin Creek and should be more buffered against stream temperature changes than smaller streams. Therefore the increases are due to some other factor, perhaps differences in riparian zone shade.

Although shade is a factor, stream gradient and the elevation at which monitoring occurs may also influence stream temperatures. In a model

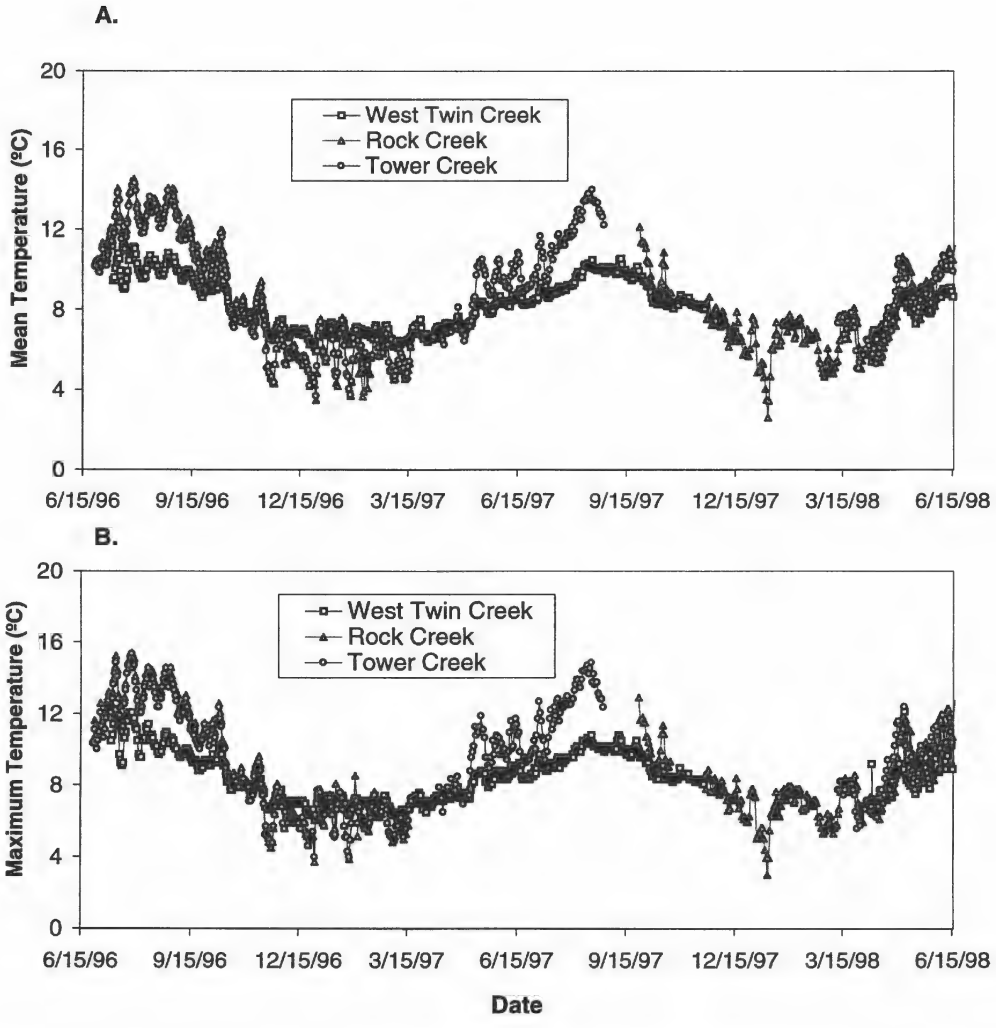

Figure 2. A. Mean daily, and B. maximum daily stream temperatures in West Twin, Rock and Tower Creeks from June 1996 to June 1998.

developed by C. Earle, Beak Consultants Inc. (unpublished), using data from 92 streams in Washington State, shade had little influence on stream temperatures at elevations below 447 m. All streams monitored below this elevation were likely to exceed 16°C, the Washington State water quality upper limit for salmonids, regardless of the amount of shade. When gradient was included in the analysis the model suggested that steep gradient streams would have a buffered stream temperature regardless of shade. All of our monitoring was done between 170–244 m. West Twin Creek had the steepest stream gradient and shortest catchment length among the watersheds (Table 1). However, from the data available to us we cannot determine if the differences in stream gradient and catchment length in our study influenced the buffering of stream water temperatures.

Stream Chemistry

pH, Alkalinity, Electrical Conductivity, Total N and Total P

There were no seasonal patterns or significant differences in pH amongst the streams and pH was > 6.5 except for the two drops seen in West Twin Creek (Figure 3A). The low pH values in West Twin Creek occurred in spring of both 1996 and 1997 and have corresponding dips in alkalinity (Figure 3B). Rainfall measured at the Hoh Ranger Station nearby the watersheds and streamflow from West Twin Creek are presented in Figure 4A and B (streamflow was not measured in the harvested creeks). The sampling dates when large decreases in pH were detected were preceded by large rain events of 191 and 202 mm in one day (only 7 out of 2291 days measured have exceeded 178 mm of rain). Streamflow data were unavailable for the first large rain event but the later event resulted in a quick response in streamflow (Figure 4B). Whitfield et al. (1993) demonstrated that storm events in a coastal British Columbia forested watershed resulted in rapid and significant decreases in alkalinity that took days to recover. Although in that study pH decreased only slightly the authors hypothesized that a larger storm could consume all of the alkalinity and pH would then decrease significantly (Whitfield et al. 1993). A large storm event may cause dilution of base flow, dominated by base cations, and an increase in subsurface flow, dominated by organic acids and nitrate, resulting in a dramatic change in stream chemistry (Whitfield et al. 1993). From autumn of 1993 through 1995, the pH of West Twin Creek was lower than the long-term average due to acidic inputs (Edmonds et al. 1998). This may have lowered the buffering capacity of the stream. The reason we do not see pH and alkalinity drops in the harvested streams may be due to: (1) lack of a thick organic layer, and (2) soil disturbance after harvesting providing more buffering capacity deeper in the soil profile. More extensive sampling of storm events and soils are needed to ascertain this.

There appeared to be little long-term influence of harvesting on stream pH, alkalinity, EC, and total N and P concentrations. Total N and P concentrations were not different among streams and were generally low ranging between 0–0.62 and 0–0.72 mg L^{-1} for N and P, respectively. Electrical conductivity was slightly higher ($p<0.0001$) in West Twin Creek (Figure 3C) than Rock or Tower creeks. The typical seasonal pattern that we have observed in the past in West Twin Creek (Edmonds and Blew 1997), i.e., high EC during low summer flow reaching a peak in September before the start of the rainy season and low values in winter, were observed in all three streams.

Cations

Calcium (Figure 5A) and Mg (Figure 5B) concentrations were consistently higher ($p<0.0001$) in West Twin Creek (averaging 777 μeq L^{-1} and 164 μeq L^{-1}, respectively) than in harvested streams (averaging 639 μeq L^{-1} and 125 μeq L^{-1}, respectively). Potassium (Figure 5C) and Na (Figure 5D) concentrations were not significantly different among streams (averaging 40 μeq L^{-1} and 161 μeq L^{-1}, respectively), however, there was a Na peak in August of 1996 in the harvested streams that was not in West Twin Creek. Sodium, Ca and Mg all varied seasonally, that is, highest values occurred in summer and fall and lowest values occurred in winter (Edmonds and Blew, 1997). Cations tend to concentrate when flows are low and are diluted when flows are high and rock contact time is shorter. The weathering of minerals, including calcite, albite, vermiculite, and kaolinite, is likely the main source of these cations (Larson, 1979). However, a large source of Na input to coastal streams is from precipitation, due to oceanic aerosols and particles. In fact Na was found to be the dominant cation in precipitation at these sites (Blew and Edmonds, 1995). The Na peak observed in August 1996 in the harvested streams may have been due to inputs from the ocean, although no unusual precipitation events occurred during that month (Figure 4A). The reason for the lack of this peak in the old-growth site is not clear; however, it may be due to the difference in distance from the ocean and watershed aspect (Table 1). It has been shown that the concentration of Na and Cl in precipitation can decrease with distance from the ocean with the largest changes occurring within 10–40 km (McColl, 1982, Blew and Edmonds, 1995). Wigington et al. (1998) also showed that Cl concentration in stream waters decreased at similar distances from the ocean. Unlike the higher concentrations of Mg and Ca found in West Twin Creek Na concentrations were not different in comparison to the harvested streams

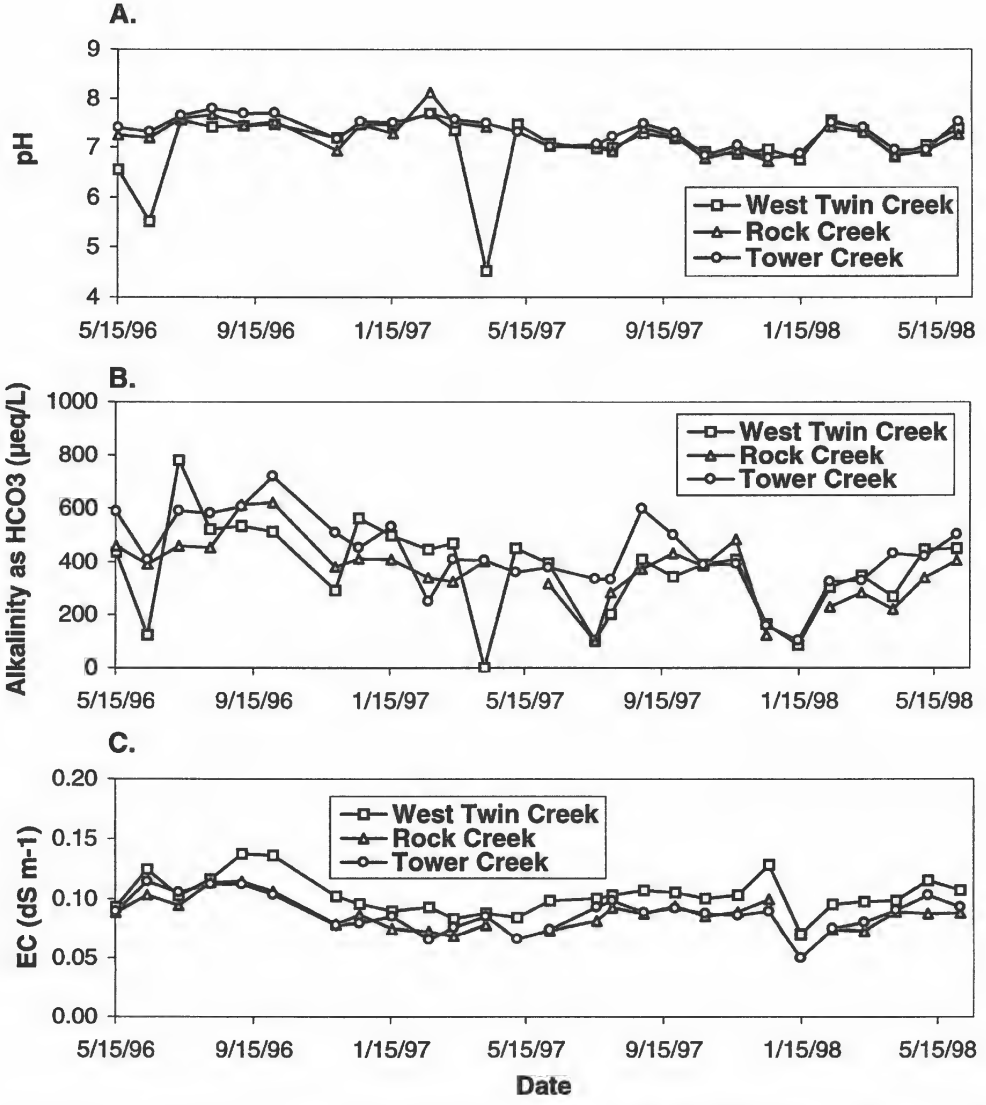

Figure 3. A. pH, B. alkalinity, and C. electrical conductivity (EC) in West Twin, Rock and Tower creeks from May 1996 to June 1998. Average EC was significantly higher in West Twin Creek than Rock and Tower creeks ($P < 0.001$). No significant differences for pH and alkalinity.

(Figure 5D) while Cl concentrations were lower (Figure 6B). The ratio of Na to Cl is also higher in West Twin Creek than the harvested streams (2.4 and 1.7, respectively), suggesting that the watersheds are influenced differently by sea salt inputs. Excess Na concentrations in precipitation, from 1984–1999 (Edmonds, unpublished data), show that it is not unusual to have oceanic influenced inputs in the summer, perhaps due to marine fog. Canopy cover is also a factor in how Na and Cl enter the watersheds. Salts can concentrate on leaves and needles during the summer

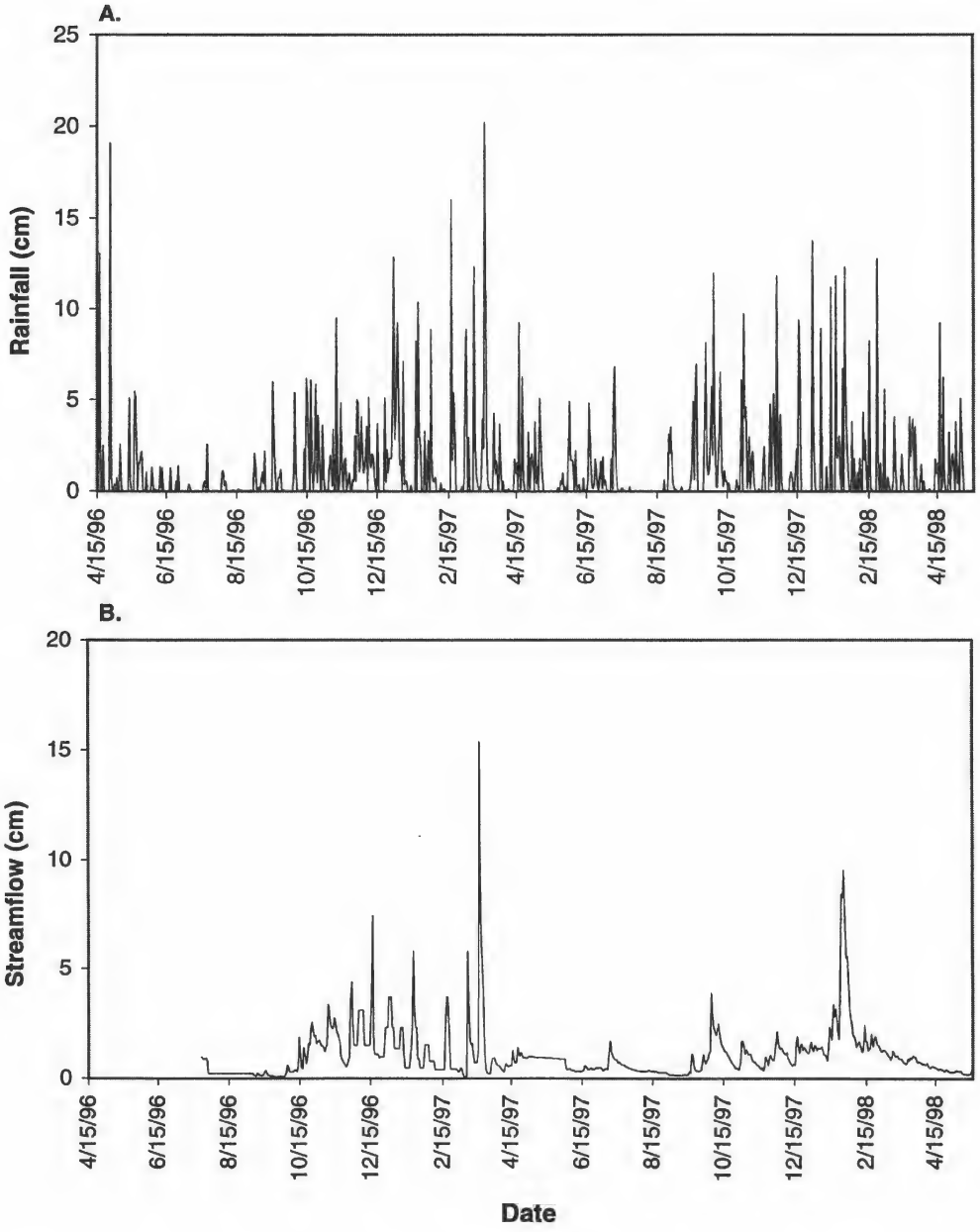

Figure 4. A. Daily rainfall (cm) from the Hoh Ranger Station and B. Daily streamflow (cm) at West Twin Creek weir.

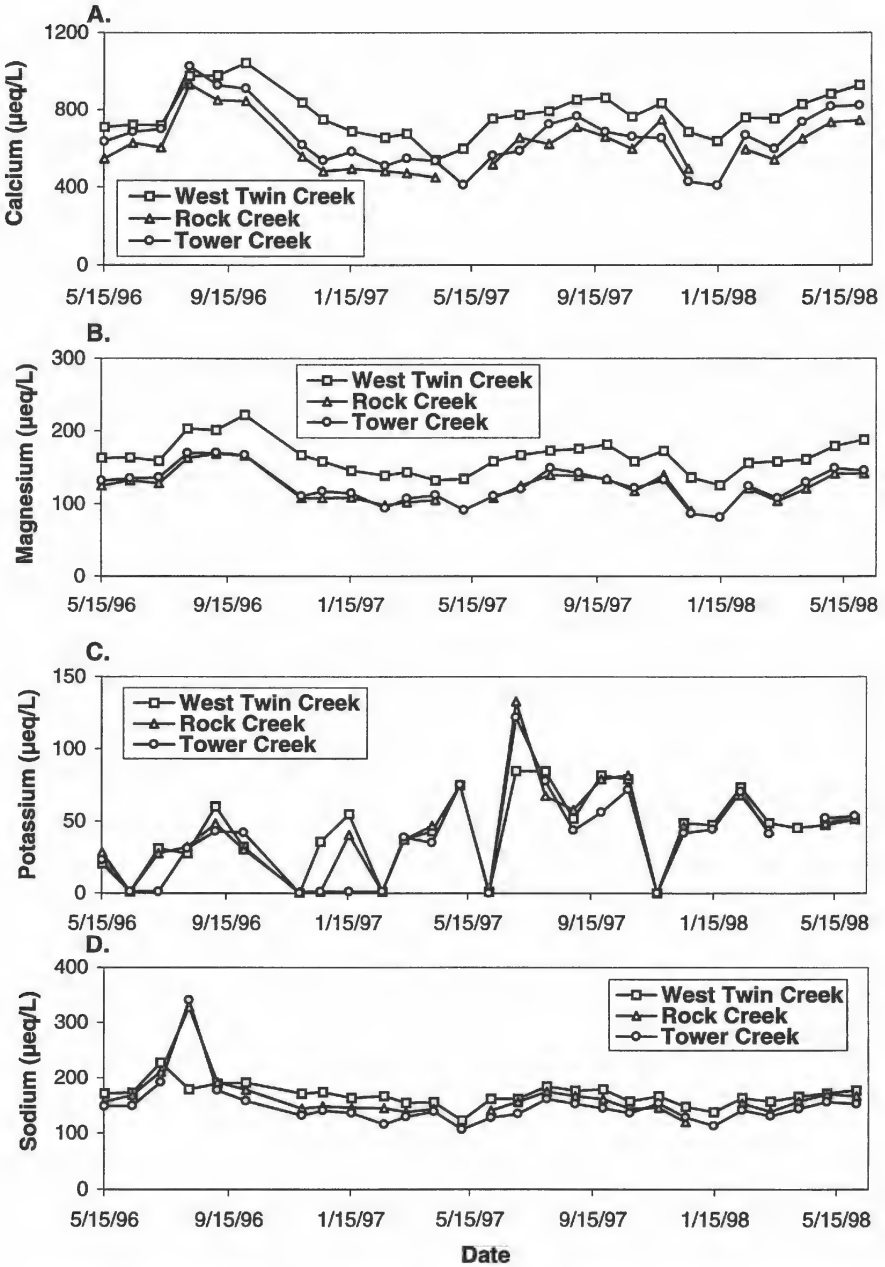

Figure 5. Concentrations (µeq L^{-1}) of A. calcium, B. magnesium, C. potassium, and D. sodium in West Twin, Rock and Tower Creeks from May 1996 to June 1998. Average concentrations of calcium and magnesium were significantly higher in West Twin Creek than Rock and Tower creeks ($P < 0.0001$). No significant differences for potassium and sodium.

time resulting in input pulses with the onset of rain. The harvested streams have red alder that hang over the stream channel, while the old-growth channel has a less dense and higher canopy.

Ammonium concentrations in all streams were low and often below detection averaging 0.9, 1.0, and 0.6 μeq L^{-1} for Rock, Tower and West Twin creek respectively. The concentrations of cations we observed were similar to those observed by Wigington et al. (1998) in coastal streams in Oregon, although our Ca, K and Na concentrations were slightly higher.

The lower cation concentrations observed in the harvested watersheds are probably due to more runoff. Harvesting can decrease the amount of evapotranspiration, and hence increase runoff, due to lower leaf area (Swift and Swank 1981) and this effect can be larger in wetter areas (Bosch and Hewlett 1982). Thinning has also been noted to decrease evapotranspiration (Aussenac et al. 1982). Evapotranspiration is low in the old growth site, averaging 22% of precipitation from 1985–1994 (Edmonds et al. 1998), and may be even less in the harvested watersheds. However, it is unlikely that differences in evapotranspiration alone could account for the differences in cation concentration. Differences in soil weathering rates may also contribute to the differences in concentrations we observed. Our results could indicate that the soil in old-growth sites are weathering faster than the disturbed sites. It may be that the amount of organic acids is higher in the old-growth soils and this may enhance weathering rates during base flow. Viers et al. (1993) found that organic acids increased weathering and solutes leaving tropical forest catchments. The underlying mineral soils and bedrock are similar in all three watersheds (Larson 1979, Edmonds et al. 1991), therefore differences in organic horizons in the watersheds may be a reasonable explanation.

Anions

There were few differences in NO_3 concentrations among the streams except during the summer of 1996 (Figure 6A). All three streams had increased NO_3 concentrations in July 1996. Concentrations in West Twin Creek then fell while they increased to a maximum concentration of 60 μeq L^{-1} in Rock and Tower creeks in August 1996. In the past we have observed peaks in NO_3 concentrations in West Twin Creek in the late summer or fall when the rainy season begins and vegetation demands are decreased (Edmonds and Blew 1997). Although the summer of 1996 was relatively dry it was not without summer rainstorms that could have mobilized the nitrate to the stream. The prolonged NO_3 pulse in the disturbed watershed may have been due to red alder in the riparian zone. Stottlemyer (1992) related elevated stream nitrate concentrations to the presence of alder vegetation in the riparian area of a stream in Alaska. Wigington et al. (1998) suggested that the high nitrate concentrations in autumn from 48 streams in Oregon were mainly due to red alder. They found concentrations NO_3 concentrations ranging from 28 to 94 μeq L^{-1} in coastal streams. The maximum concentration we found in Rock and Tower creeks was 60 μeq L^{-1}.

A seasonal NO_3 peak was not observed in any of the three streams in 1997. This also was observed in a nearby Queets tributary (Bechtold et al. 1999). We hypothesize that the pattern observed in 1997 was due to excess rains during an El Niño that kept soils moist throughout the summer (Figure 4A), not allowing the buildup of nitrate. Others have found that stream NO_3 concentrations vary seasonally and often peak with increasing flows during spring snowmelt (Foster et al. 1989, Arheimer et al. 1996). High stream NO_3 concentrations were observed at a site in Wales after a warm and dry period followed by increased rain (Roberts et al. 1984). These studies and our results emphasize the influence of the hydrologic cycles on nitrate leaching.

There were no significant difference in alkalinity (Figure 3B), Cl (Figure 6B), and PO4 (data not shown) among the three streams and concentrations were similar to those found by Wigington et al. (1998) in coastal streams in Oregon. However, alkalinity did decrease significantly in West Twin Creek when pH decreased in the spring of 1996 and 1997, as discussed earlier. Sulfate and silica concentrations were significantly higher ($p<0.0001$) in West Twin Creek than Tower and Rock creeks (Figure 6C and 6D), however, seasonal patterns were similar between streams. For sulfate the highest concentrations were observed in the summer. Sulfate is present in the bedrock material of this area and the major source to these streams is weathering (Larson 1979). Silica

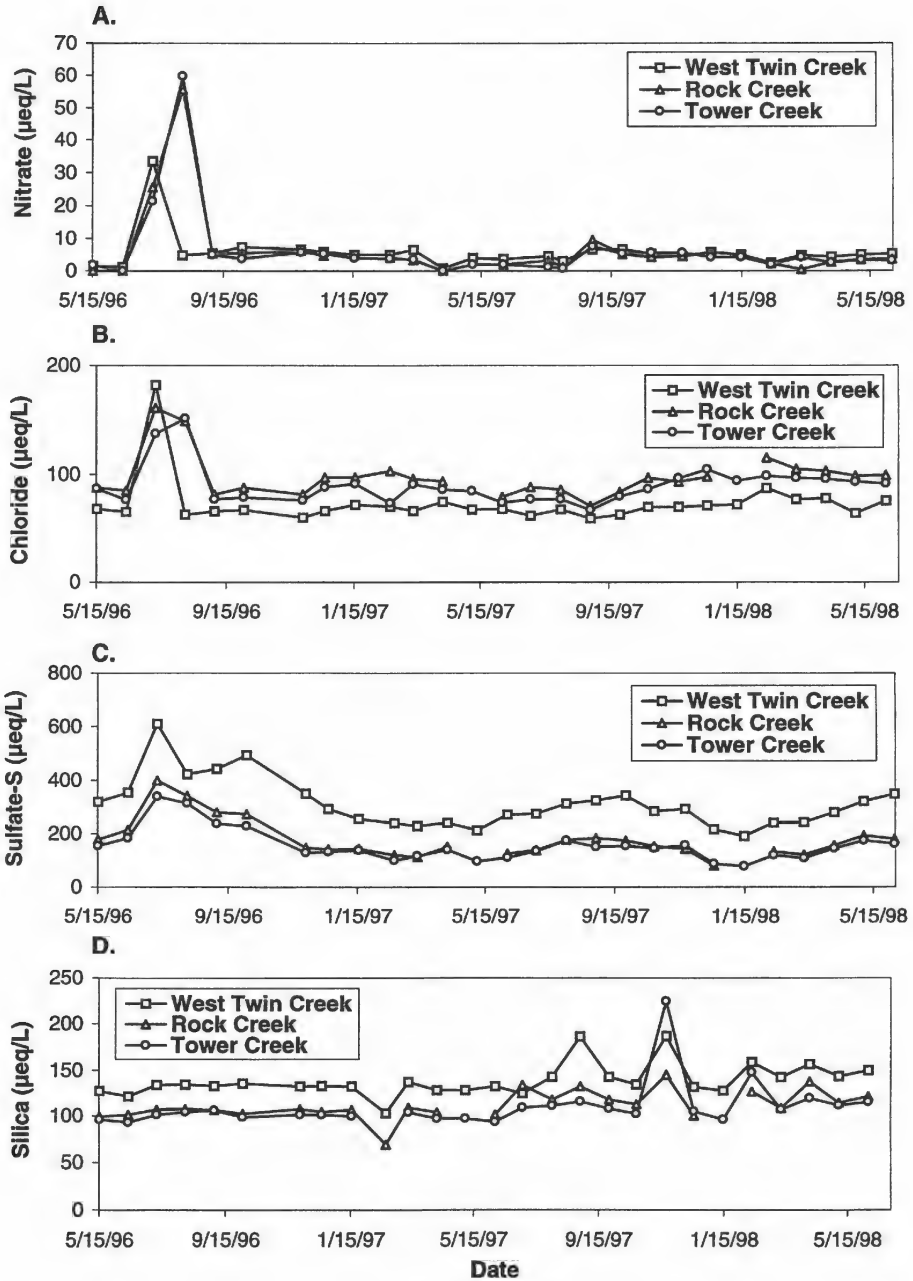

Figure 6. Concentrations (µeq L^{-1}) of A. nitrate, B. chloride, C. sulfates, and D. silica in West Twin, Rock and Tower Creeks from May 1996 to June 1998. Average concentrations of sulfates and silica were significantly higher in West Twin Creek than Rock and Tower creeks ($P < 0.001$). No significant differences for nitrate and chloride.

concentrations did not have a seasonal pattern. Similar to the cation concentrations the difference observed in sulfate and silica are likely due to differences in runoff and weathering.

Stream turbidity

Concentrations of suspended sediments can increase after forest harvesting and road construction, but not always (Binkley and Brown 1993). Turbidity data for Rock, Tower and West Twin creeks are shown in Figure 7. Turbidity was low and not significant among the streams, averaging 1.06, 0.89 and 0.83 NTU for Rock, Tower and West Twin creeks, respectively, which is typical for Northwest streams (Binkley and Brown 1993). In the winter of 1997–1998 turbidity in all three streams increased, with maximum values of, 3.63, 4.37 and 4.63 NTU for Rock, Tower and West Twin creeks, respectively. This was likely due to storm events and higher flows. In a study in California by Bolda and Meyers (1997) turbidity increased during storm events. Although there were no increases due to disturbance, variability was greater in disturbed watersheds. In addition, suspended sediments were significantly higher in one year. The discrepancy between turbidity and suspended sediment measurements was due to larger soil particles derived from the sandy loam soil increasing the mass but not the refractive properties of the samples (Bolda and Meyers 1997). Fowler et al. (1988) found an increase in turbidity and suspended sediment immediately after road construction in harvested areas, but little after that.

Conclusions

Partial harvesting of 7–33% of the land area in the Rock and Tower creek watersheds resulted in only small influences on stream temperature, chemistry and turbidity 11–15 years after harvesting. This suggests that partial harvesting may be a successful aspect of ecosystem management with respect to streams. Maximum stream temperatures increased by only about 3°C in the harvested streams compared to the unharvested old-growth site and were more seasonally variable. Stream temperatures did not exceed 16°C in any stream and therefore salmonid species are not likely to be affected; there were no salmonids in our streams. There were some significant differences in concentrations of some cations, anions and EC between

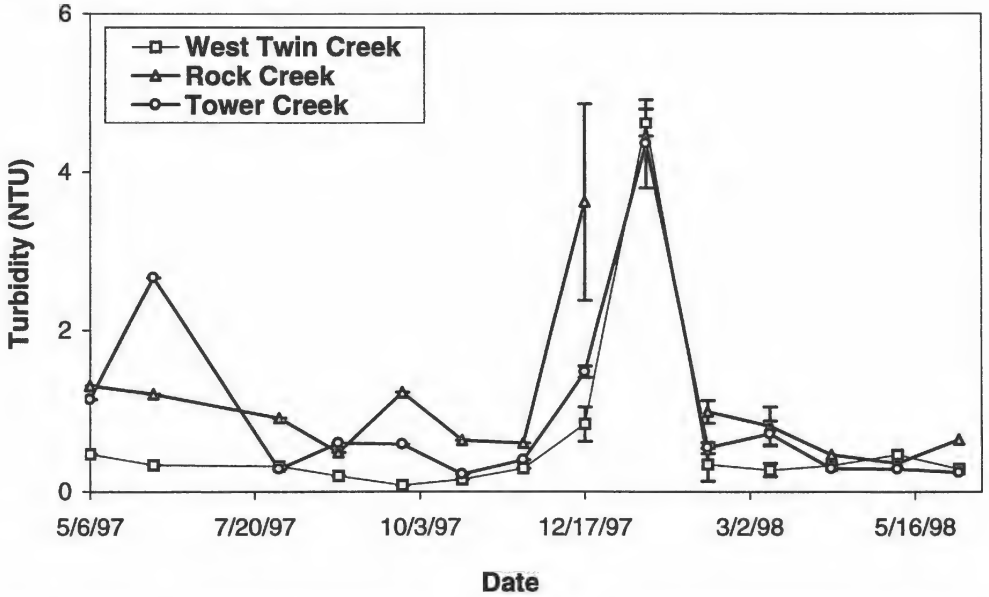

Figure 7. Turbidity in West Twin, Rock and Tower creeks from May 1997 to June 1998. Error bars are standard deviations. Average turbidity was not significantly different among watersheds ($P < 0.001$).

the old-growth and the partially harvested watershed streams, but in most cases concentrations were actually higher in the unharvested watershed. Average nitrate concentrations were not significantly different among watersheds, although the highest nitrate concentrations were observed in the harvested watersheds. Red alder in riparian areas may be contributing to the higher nitrate in the disturbed watershed streams. Stream turbidity was not significantly higher in the harvested watersheds. However, our study did not address the effects of logging that can occur within the first few years post harvest such as increased siltation and nitrate pulses that have been documented at other sites (Binkley and Brown 1993).

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Thomas J. Mills, USDA Forest Service, Pacific Northwest Research Station, 333 SW 1st Avenue, Portland, Oregon 97208-3890

Position Advocacy by Scientists Risks Science Credibility and May Be Unethical[1]

The demand for science information in decisions about the management of natural resources is ever more insistent, just as the debates seem ever more contentious. Increasingly, research scientists from public agencies such as the USDA Forest Service are being asked to bring science information to the decision-making table. Research scientists are being asked because of their expertise and because they generally are viewed as objective and independent from interests advocating different solutions in the debate. These perceptions of credibility in turn come from the public's trust in the scientific method and science institutions.

Scientists and the science information they bring can make many valuable contributions to the decision-making process. They can contribute an understanding of the system being managed, understanding that is essential to intelligent development of management options and to the reasoned estimation of the effects of management actions. Once management goals are established by the decision maker, or through whatever process is legitimate, scientists can contribute to development of management options that might achieve those goals.

The scientists also can estimate the consequences of management options, including the uncertainty in those estimates and risks inherent in the management option. It may be challenging for the scientist to estimate the consequences of management options that they helped create, but it is a valuable and legitimate role as long as the estimates are clearly based on the available science information.

The scientist likely will have to make professional judgments when estimating the consequences of management options, because a complete array of hard science studies on which to base the estimates probably is not available. For example, scientists may have to interpolate between points of hard science information, extrapolate results from the research study area to another area, or from one geographic scale to another. None of these science roles is easy, but they are feasible when done with careful anchoring in the scientific literature and when associated with clear communication of the degree of confidence in the results.

[1] This paper was originally published in *OSU Reflections,* a newsletter from the Oregon State University Department of Philosophy. The author has modified it slightly in this version.

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Accomplishing these science roles is essential to informed public decisions. Science information sometimes provides a neutral ground where people with divergent interests can assemble to better understand the systems about which they have an interest. Without the science information, the public dialogue often deteriorates into a dogmatic debate among divergent and often mutually exclusive positions driven by self interest. Such a dialogue is not likely to yield a full array of potential management options and will surely lack a full understanding of the consequences of any of the options. Inclusion of science information may also allow participants to generate options that are more acceptable to individuals representing diverse interests. Moreover, these options may not arise in the absence of scientific input.

In playing these science roles in decision-making settings, it is appropriate that the scientist forcefully advocate the consideration of the relevant scientific information. Especially once science has been engaged in the debate, it is even the responsibility of the scientists to advocate for the full consideration of scientific information and to not allow others to pretend that the science was considered, if in fact it was not.

One way of implementing this is for scientists to conduct what might be called a "science consistency check," wherein they evaluate whether the final decision fully considered, correctly interpreted, and revealed what is currently known from the available science information. Such an evaluation can facilitate holding everyone accountable for considering the science. And this means that all the available scientific information is considered, not just some subset on which decision makers might want to focus because that subset seems to support their final decision.

This science consistency check of the decision can be a powerful tool in ensuring the full consideration of science, even recognizing that science information is only one of several factors to consider in any decision. It is an effective tool in helping the scientists discipline themselves to stay in a science role. It can also become a useful vehicle for effectively communicating the essence of the science information into the decision process, albeit at the risk of confrontation between scientists and decision makers.

The next question, though, is whether the scientist should advocate a particular management option as the *best* solution, either because the scientist has strongly held personal values or because he/she thinks their science perspective gives them special insights that others lack. The most important consideration in answering this question is how position advocacy affects the vitality of the science component of the decision.

Invariably, any natural resource management decision is a value-based balance among diverse considerations, of which science information is but one component. Even though a balance among diverse values is the central stuff of decision making, it is not the stuff of science. Science informs the choice, but it does not make the choice or direct a single solution.

This is not to say that scientists do not have personal values: they do. It also is not to say that those values do not affect the scientist's behavior: they do. Personal values affect what scientists perceive to be important to study, how they present their research findings, and how they integrate different pieces of scientific information into a larger scientific whole.

At issue is not whether scientists have personal values. Rather, it is whether they should express those values by advocating for any particular decision outcome during a public debate in which they are being counted on to be a neutral provider of credible science information.

Position advocacy by scientists can take at least two forms. In the first form, the scientist advocates a position while pretending that the position is a science statement rather than a personal value statement. If science has any credibility in the debate, the scientists might do this to gain more attention and support for their personal position. This misrepresentation of personal values as if they were science is unethical. It is just as unethical to misrepresent personal values for science, as it is to misrepresent experimental data or the results of statistical test in a scientific paper.

And it is a misrepresentation whether the scientist initiated the position advocacy or was asked by someone else to do so; for example, a decision maker might ask the scientist to endorse a decision. If that endorsement is anything other than an answer to the question of whether the decision was consistent with science, (i.e., the science consistency check), the endorsement is a misrepresentation; it is just as much of a

misrepresentation as if the scientist originated the advocacy themselves. And the decision maker shares the responsibility for the misrepresentation.

The second form of position advocacy is more problematic. In the second form, the scientist carefully clarifies that they are expressing a personal value rather than science information when they advocate a position. They make it clear that they have taken off their science hat and put on their personal value hat. At best, the audience will be confused about whether the scientist is speaking science or personal values. The confusion is not helped if the scientist wraps their advocacy in scientific language. Most likely, the public will think, at least at first, that the personal value-based advocacy is really science information because, after all, the scientist gained the public platform through their scientific standing, not personal values. If this confusion occurs, the effect of the second form is the same as the first, that is, a misrepresentation, even if the intent is different.

What is the outcome, whether the misrepresentation was intended or not? Although arguably the outcome might be different from different perspectives, from at least one perspective the outcome will be erosion of the scientist's personal scientific credibility along with the credibility of the science information they brought to the dialogue. How can they be trusted to be a neutral source of science information if they entangle science with value-based advocacy, intended or not? That credibility damage might wash over onto other science information vital to the debate and perhaps even the institution of science itself.

Personal values and the advocacy of those values are vital components of any substantial natural resource management debate. They also are common components of most debates. There never seems to be a shortage of advocates for different solutions. Credible scientific information about system function, feasible management options, and inherent risks and consequences of different management options, on the other hand, is usually in short supply. Yet, it too is a vital component in reasoned public choices. Sacrificing the scarce science contribution for the more common, though no less important, expression of personal values is a poor trade. It is a poor trade for the credibility of science and it is a poor trade for the decision-making process.

Given these risks and tradeoffs, scientists should avoid position advocacy. Scientists should even avoid recommending an outcome or decision. The scientist can get to a recommendation only by doing the same value-based integration of divergent considerations as they would if they advocated a position. Therefore, a recommendation is likely to be seen as position advocacy, and reasonably so. Also, attacks on the scientist's recommendation could easily lead the scientist to defend the recommendation and thereby slide further down that slippery slope into advocacy and further lose the objectivity on which their scientific credibility is based.

This discussion has thus far focused on research scientists with public agencies. Should the same guidelines apply to scientists in other organizations, such as scientists with universities, private sector firms, and special interest groups? Similarly, should they apply to staff specialists in public agencies, like a regional hydrologist or a state fish biologist, who represent themselves as scientists? Given that interest groups and private-sector firms were formed to pursue specific agendas, perhaps different guidelines are appropriate.

The answer is a function of whether the scientists in these other organizations can credibly play two roles simultaneously: that of credible, neutral scientist and that of position advocate. The answer is that they cannot — not any more than a public research scientist can. There is nothing wrong with advocacy and there is nothing wrong with bringing science to the debate, but there is a great deal wrong with pretending that a selective use of available science to support a position or the value-based advocacy of a particular position is science or that science information somehow points to one solution. They cannot credibly change hats any more than public agency research scientists can. Therefore, yes, the same guidelines should apply and for the same reasons.

It is good that scientists have passion for sound, science-based decisions. Their passion for good decisions should be focused on assertively communicating the rich fabric of science information into the decision process. It should not be translated into an indulgence of personal values or into thinking that their experiences give them unique insights that all others lack. Alternatively, the individual can stop playing a science role altogether and play solely an advocacy role. Play one role or the other, but not both.

An attempt by the scientist to simultaneously be a science information provider and a position

advocate is an inherent conflict of interest. The development of objective science information on the one hand and the value balancing of all considerations in a final decision on the other hand are two different roles than cannot be credibly played by one person. The risk to the credibility of the science component of the decision process is too great. At best, it will further confuse already contentious and complex public debates. At worst, it is an unethical misrepresentation of personal values as if they were science information.

Book Reviews

Continental Conservation: Scientific Foundations of Regional Reserve Networks

Michael E. Soulé and John Terborgh, editors. Island Press, Washington, DC. 227 pages 1-55963-697-1 (cloth), 1-55963-698-X (paper) $50.00 (cloth), $25.00 (paper)

For nearly a decade, the Wildlands Project has advocated a new approach to conservation, the protection of living nature at regional and continental rather than political scales. Project goals are "... to honestly and boldly say what is necessary to save living nature in North America..." (page xi), to state clearly what conservation biology and conservation biologists *should* be doing. *Continental Conservation,* a creative synthesis of the science relevant to those two goals, is a product of a 1997 Wildlands Project workshop attended by thirty invited experts in conservation biology, wildlife biology, and ecology. Participants were heavily skewed toward terrestrial systems. More than a third were mammal ecologists, none were stream ecologists, and only two were marine ecologists. In many contexts, illustrations from aquatic systems could have strengthened and broadened both the principles and the lessons.

Six timely and creative syntheses of contemporary knowledge relevant to regional and continental scale conservation are flanked by introductory and summary chapters by the editors. Manuscript development began at the workshop and continued for nearly a year as collaborations of 7 to 15 authors (x = 9.7).

The editors' (Chapter 1: "The Policy and Science of Regional Conservation") set the stage with enticing sections heads such as "Thinking Bigger," "The Scale of Things," "Top-Down Regulation," and "A Vision and a Challenge." They acknowledge that not all conservation challenges are amenable to regional or continental scale efforts; at the same time, some of the most important conservation challenges (e.g., preservation of top carnivores) can only be dealt with at those scales.

An exploration of scale (Chapter 2, "The Issue of Scale in Selecting and Designing Biological Reserves" by Michael Scott and 10 others) yields several principles for the design of nature reserves, some obvious, others not so obvious. Conservation programs organized to protect bears, for example, may preserve field mice, but those designed to protect field mice are not likely to protect wide-ranging species such as bears. Such asymmetries are often ignored. Abiotic features that organize communities often operate at scales much larger than the scale at which the organisms and biological processes operate. Conservation programs should not overlook the importance of size, frequency, and intensity of disturbances in the evolution and maintenance of the regional biota.

Theory and empirical evidence points to the keystone role of top predators as stabilizers of the trophic structure of terrestrial ecosystems (Chapter 3, "The Role of Top Carnivores in Regulating Terrestrial Ecosystems"). Terborgh and 6 co-authors stress the importance of retaining intact faunas to permit ecological processes to operate unhindered. They conclude that legislated efforts to control extinctions (e.g., Endangered Species Act) will often be overwhelmed by irresistible biological forces set in motion by the loss of predators.

Any effort to create a regional reserve network will likely involve efforts to restore degraded areas. "Regional and Continental Restoration" (Chapter 4) emphasizes the importance of defining project specific restoration goals. They also highlight the importance of restoring both lost parts and altered processes of degraded areas and, especially, the need to control nonindigenous taxa. Ten authors, led by Dan Simberloff, wisely recognize two critical points: (1) Any restoration action must be grounded in careful analysis of local context, biotic and abiotic, and human goals, (2) Social and legal impediments to restoration add significantly to the challenges faced by conservation biologists.

Any comprehensive conservation strategy must have "Core Areas: Where Nature Reigns" (Chapter 5), places where biodiversity, ecological integrity, or wilderness take precedence over other values

and uses. Noss and six co-authors caution against relying on economic arguments to justify these crucial conservation areas and conclude that conservation strategies that lack meaningful core areas are naive, arrogant, and dangerous. They are especially critical of management proposals for Pacific Northwest forest.

Corridors to reconnect fragmented landscapes can be both a boon and bane to conservation goals (Chapter 6, "Corridors: Reconnecting Fragmented Landscapes). The 15 authors of this chapter, led by Andy Dobson, provide much timely guidance about the advantages of corridors as well as the controversies that make corridors difficult to implement. The latter includes their role as corridors for movement of infectious disease, their vulnerability to edge effects, and the political costs of changes in land-use that may be required to increase landscape connectivity.

Increased understanding of the sensitivity of nature reserves to land use and human activities in adjacent areas has stimulated calls for buffer zones around reserves. In Chapter 7 ("Buffer Zones: Benefits and Dangers of Compatible Stewardship"), Martha Groom and seven co-authors define buffers and note that some activities may be suitable in buffer zones while others can cause serious damage to nearby core reserves. They frame a series of questions that should be considered in design, use, and management of buffer zones and suggest incentives to encourage "biodiversity-friendly" behavior among those who own, live in, exploit, and use areas adjacent to core areas.

The editorial team returns in Chapter 8 (Why We Need Megareserves: Large-Scale Reserve Networks and How to Design Them") urging readers to commit more time to the challenge of saving nature; few developed countries still have the opportunity that we have in North America. They conclude that large landscapes must be protected. Management practices need major reform, top carnivores must be restored, and alien taxa turned back. Wildness must be returned to disturbed and degraded habitats, and physical disturbances such as floods and fire must be given free run to rejuvenate plant communities and shape landscapes.

One substantive lapse deserves mention. Despite repeated recognition of the tentative nature of many of their detailed recommendations and strategies, no chapter deals with the need to assess and evaluate their prescriptions by routine monitoring of program effectiveness. Words such as *assessment, monitoring,* and *evaluation* do not occur in the index. Failure to incorporate such assessments will limit conservationists' ability to understand which prescriptions are successful and which are not.

Authors and editors of this volume have done a fine job weaving together theory, empirical evidence, and practical guidance, including the pivotal role of social, political, and economic forces in conservation success. They reinforce the importance of the Wildland Project vision and provide the technical foundations to move its agenda forward.

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Irrigated Eden: The Making of an Agricultural Landscape in the American West

Mark Fiege, 1999, University of Washington Press, Seattle, Washington, 323 pages
ISBN 0-295-97757-4 ($35.00)

Author Mark Fiege understands history. He also understands ecology, infrastructure, and hydrology. This rare combination of diverse understandings has resulted in a book that is both entertaining and educational in describing how one part of the western U.S. (the Snake River basin) came to look and behave as it does today in terms of ecology and irrigation and water resources development.

Irrigated Eden reconstructs the chronology of diversions of water from various reaches of the Snake River system in southern Idaho and examines the motivations, objectives, desires, and personalities of individuals making those diversions. The book examines the final outcome of water diversions for irrigation in terms of their impacts on the flow systems of the Snake River, on the nature and diversity of flora and fauna both in the riparian corridors, and on the watered landscape. It also describes the relative success of the developments in producing a profitable and sustainable human culture and on creating the governmental infrastructure that now supports the system. An impressive one-third of *Irrigated Eden* is devoted to annotated footnotes and bibliography drawn from a myriad of archives stashed throughout southern Idaho. The footnotes constitute a valuable trust of insights into ways of thinking and self-discovery by the irrigated culture that evolved in and settled southern Idaho.

Several themes and realizations, besides history of irrigation development, thread their way through *Irrigated Eden*. One of these is the impact that irrigated agriculture has had and continues to have on the ecology of the Snake River basin of southern Idaho. Another is the hydrologic impact of irrigated agriculture on the water resources of the region. A third theme is the "struggle" or "journey" of man "against" nature that was a large part of the attitude and outlook of the early developers. Fiege couples this third theme, however, with the parallel and somewhat balancing fourth theme of man "completing" and "evolving" nature by uniting the potential of the soil and land with the potential of water to create an irrigated "garden of Eden." However, he labels this "Eden" theme as a "myth" toward the end of the book.

The book begins by describing the author's personal observations and realizations that entrain both ecologic and hydrologic change and evolution of the southern Idaho landscape resulting from the initiation of irrigated agriculture. Most of these changes are visible to anyone. However, the reason and cause for them is not obvious to many until pointed out by the author. The first part of *Irrigated Eden* shows much of the negative side of the hydrologic consequences of man's manipulation and evaporation of the mighty Snake River system. However, rather than stop at this point and merely create fuel for a one-sided outlook on the nature and results of man's fiddling with nature's original system, Fiege continues to provide other outlooks on what has transponded from man's holding and spreading of nature's water over her own dry landscape. Two statements from the book that help to describe the image that the author attempts to paint in the mind of the reader are the following:

"Thus we should view each place that we inhabit, Idaho's irrigated farmland or any other, not simply as a departure or degradation but as a new environment, a new ecological system, that has been created and formed." "... in its place stands a new, hybrid landscape that should be understood on its own terms."

The book's chapters are titled to provide good indication of the viewing angles taken by the author. Besides a well written introduction, chapter titles are "Genesis," "Habitat," "Dividing Water," "Labor and Landscape," "From Field to Market," and "Industrial Eden." Fiege attempts to insure that the reader catches the main focus and intent of each chapter. He provides several pages of "review" and summary at the end of each chapter. However, in many cases, a single paragraph would probably do. Near the end where the book is describing the myth and metaphor of a perfect Eden that was to have been created by irrigated agriculture, it seems to be a bird circling slowly to land but unable to select the spot. Repetitions of common thoughts, perspectives, and ideas leaves the reader somewhat anxious to make a conclu-

sion and ending. Other than this circling, however, *Irrigated Eden* unfolds and forges along the intended pathlines of historical documentation and ecologic and hydrologic education.

In light of the current dialogues and assessments of the impacts of the consumption of upper Snake River water on the health of the Salmon populations of the lower Snake River system, *Irrigated Eden* provides little information or perspective on direct impacts or relationships between the two. It does, however, offer good images and descriptions to help one realize some of the positive impacts that irrigation in the upper Snake has had on increased recharge of ground-water systems and subsequent increased flows of springs back to the Snake system, with much of the increased flows occurring during drought and other low flow periods. Fiege does well in balancing these favorable impacts on low flows in the Snake system with stark descriptions of the Snake River at times completely dry in both the Blackfoot and Milner stretches due to complete diversion of the river into canals.

Irrigated Eden should be required reading for anyone who wishes to enter the debate of modifying water diversions by irrigated agriculture to facilitate other beneficial uses of water including recreation, fisheries, riparian habitat, and salmon. The book does not attempt to sway the reader one way or another in regard to what is best or worst. It does describe very well the background and context of irrigated development, the culture that it created and supports, and many of the latent benefits and detriments that irrigation development has had on the landscape in both ecological and hydrologic contexts. It is a book for environmentalists, wildlife managers, engineers, politicians, and teachers to sit down with, read, and ponder the ways and means of the present agricultural system in southern Idaho. There are many nuggets and tidbits that the reader will enjoy laying on her or his friends regarding settlement and development of Idaho.

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The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods

Edited by Reed F. Noss, Save-the-Redwoods League and Island Press, Washington, D.C. and Covelo, CA, 340 pages.

ISBN 1-55963-725-0 (cloth) $60.00, and 1-55963-726-9 (paper) $30.00.

"Redwood trees have few dangerous enemies; once established, they can grow for a very long time with the possibility of becoming among the tallest and most massive trees on earth." This sentence from the conclusion of the fourth chapter of *The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods* reiterates a sentiment that was once used to explain to me why there was (apparently) so little research conducted on redwood trees and forests. Whether or not this explanation was based on fact twenty years ago when I first heard it, this book dispels any remaining impression that research in redwood forests has been unproductive either then, or for the last two decades.

The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods offers a rare synthesis of information related to a single vegetation type, the coast redwood forest. The stated objectives of this book are ambitious. To quote the editor, "This book is meant to provide the scientific basis for ¼ protection, restoration, and sustainable management of the redwood forest." According to the editor's preface, this book was developed at the instigation of the Save-the-Redwoods-League. The League intended to create a book that could be used as a general reference for anyone interested in the coast redwood forest; but it was also intended as a guide for the League itself for making decisions regarding land acquisitions and the League's master plan. The editor explains "With a general science and conservation audience in mind, we have tried to avoid being overly technical. At the same time, however, we strove to provide sufficient technical explanation for the book to be useful to professionals and students in the biological and natural resources sciences. I believe that the editor and authors reasonably met their goals of writing a book accessible by a broad audience.

The book is organized into nine chapters, the first and last of which provide synthesis and summary by the editor, Reed F. Noss. The remaining seven chapters fairly comprehensively divide up the multifaceted information and understanding of the coast redwood forest as it stands today. Each of these chapters is a mix of summary of past literature and lore, as well as a more thorough treatment of recent work, both published and unpublished. Most chapters identify areas of needed continuation, expansion, or new research. The chapter on history summarizes and synthesizes both the paleoecological science and sociocultural history as it bears on redwoods and redwood forests. It ends with a lengthy accounting of the conservation movement related to coast redwood. A chapter on the characteristics of redwood forests provides a kind of a site description for the coast redwood region summarizing geographic range, climate, physiography, and vegetation patterns. There is a fairly detailed summary of recent work on the animals and plants found in the redwood canopy. This chapter contains several potentially useful species lists including: exotic plants potentially threatening in redwood forests; a checklist of vascular plants found in the redwood forest at Van Damme State Park, Mendocino County, California; fungi associated with redwood; lichens of the central redwood forest region; and two lists identifying rare, endangered, or globally, federally or state listed vascular plants.

The next chapter describes the life history of redwood trees, provides some new and recently published information on old growth redwood tree architecture, summarizes what is known about redwood genetics and how redwood is influenced by environmental factors, and examines disturbance regimes including brief treatments of fire, wind, flood, insects, animals and fungi.

A chapter on terrestrial fauna of redwood forests summarizes what is known about invertebrate and vertebrate faunas. This chapter provides sound justification for new substantial research efforts in this area. The concluding three "case studies" of this chapter, on invertebrates, carnivores, and marbled murrelets, provide compelling evidence both for conservation efforts, and for more research.

Aquatic ecosystems of the redwood region are the subject of a separate chapter focusing on relatively small streams originating and entering

the ocean within the coastal redwood zone, while referencing relevant research from the larger riverine systems that transect the redwood region. Summaries are provided related to watershed level processes, riparian vegetation, large woody debris, disturbance, and aquatic biota. Pristine conditions are compared with stream ecosystem processes resulting from timber harvesting and related activities. The chapter ends by identifying research needs specific to the redwood region, and reminding us that "Much work remains to be done to reverse the decline of the aquatic and riparian ecosystem in the redwood region."

Turning from science to social issues, the next chapter addresses conservation planning in the redwood region. It proposes an approach patterned after the planning process already being conducted in the adjacent Klamath-Siskiyou ecoregion. The authors describe conservation planning as "a process of evaluating the capability or suitability of different areas in a landscape for different land uses, then allocating each area to the best possible category of use." They propose using a "focal area identification and assessment model" to initiate conservation planning.

The proposed approach to conservation planning is followed by a chapter on managing redwoods for both preservation and utilization. The treatment of management of redwood parks reminds us that management is necessary even when our goal is preservation. Traditional silvicultural systems are reviewed, particularly in relation to their influence in shaping the second and third growth redwood forests existing today. Current new silvicultural approaches such as shifting mosaic of variable-size patch cuts and variable thinnings are described and proposed as the silvicultural systems of the future. This chapter ends on the note that moving silviculture toward ecological sustainability will require adaptive management, monitoring, and primarily, humility – the recognition that we do not have all the answers, and that everything we do is an experiment with uncertain outcomes.

The final chapter is a brief summary of "lessons from redwood," by the editor. It succinctly summarizes the most important conclusions from the preceding chapters. It ends with a sincere plea for protection of biologically significant stands of redwood, including all remaining old growth, for restoration of degraded redwood forest to old growth conditions, and for truly sustainable management of appropriate redwood stands for timber and other values.

This book clearly has a viewpoint favoring preservation of old growth and old growth values throughout the range of redwood, and adaptive sustainable timber management. This book was not intended to serve those who view redwood primarily as an exploitable resource who are looking for economically more efficient ways to grow redwoods faster.

One strength of this book is that it attempts to smoothly integrate and synthesize information into coherent treatments following substantive topics or themes, unlike so many books that are mere collections of technical research papers. In most ways, this book succeeds in providing a coherent treatment. In a few instances, however, the complexity of the topics, and the multiple authors resulted in contradiction, redundancy, or disorganization. For example, the volume of the largest coast redwood tree is reported on three contiguous pages three times, once as 1037 m^3, and twice as 1045 m^3. Several times, Yurok Indians are written of as if they were the only group of native people living within the bounds of redwood forests. At least Tolowa, Wiyot, Bear River, Mattole, Shelter Cove Sinkyone, Coast Yuki, Pomo, Coast Miwok, and Costanoan, and maybe others shared the region. Several tables and figures lack attribution, and some are missing important information. For example, Figures 4.6, 4.7, and 4.9, provide us with a weak "(See text for details.)" without attributing the figures themselves to any original publication or indicating the source of the data if this is the original place of publication. Table 4.3 reports nutrient levels in soils, but fails to give units rendering the table useless in comparison to any other known nutrient levels. At least this table contains an appropriate citation. On the other hand, some of the tables and figures provide much needed clarity. For example, Table 2.1 (while it fails to give a complete reference for "Geologic Society of America") provides a succinct, clear, and useful summary of the evolutionary history of redwood. As a technical reader, I would have preferred the editor and authors to have more rigorously identified both text and illustrative material as to source.

This book makes significant progress towards meeting the ambitious goal of the editor and au-

thors, "to provide the scientific basis for _ protection, restoration, and sustainable management of the redwood forest." While I think that it provides an excellent contribution to the literature on redwood forests, and provides an example of the kind of synthesis and integration needed for forests of all types, there are important parts missing. This book does a solid and nearly comprehensive job of summarizing the taxonomic entities of the redwood forest at multiple scales. I would hope that a complete understanding of a forest ecosystem would include attention to ecological processes at multiple scales also. Missing here is significant attention to ecosystem level processes (for example, production, carbon storage, nutrient cycling, and hydrology), and to stand and organism level processes (for example, specific aspects of production including photosynthesis, respiration and metabolism, carbon storage and allocation, nutrient uptake, assimilation and allocation, and decomposition). Understanding ecosystem, stand, and organism level processes such as these provides important keys to understanding and mitigating against cumulative impacts, not only of logging, but of regional and global threats to the redwood forest like acid rain and other forms of air pollution, urbanization, global warming and ozone depletion.

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The Eat-A-Bug Cookbook

David George Gordon, Ten Speed Press, Berkeley, CA, 136 pp.
ISBN 0-89815-977-6 $12.95

The subtitle of this book, "33 ways to cook grasshoppers, ants, water bugs, spiders, centipedes, and their kin" tells what the reader would expect from a book with a title *The Eat-A-Bug Cookbook.* What the title and subtitle don't indicate is some of the great general information on insects and other arthropods that is included. This information makes the book both entertaining and educational. But the book is not for the squeamish either, when the author gets into the details of preparing and consuming "bugs." The book is a good introduction into entomophagy, the practice of eating insects and other arthropods.

The book is divided into an Introduction "embracing entomophagy" followed by four parts containing nine chapters and a final valuable section, on resources. Part One "Don't worry, be hoppy: nine culinary leaps of faith, using crickets, grasshoppers, and their kin" discusses recipes for using Orthoptera. Part Two "Togetherness: A selection of social insects—bees, termites, and ants—for special occasions" includes the Hymenoptera and Isoptera. Part Three "Who's bugging whom? Eight ways to turn the tables on home and garden pests" covers Lepidoptera larvae and again the Orthoptera. Part Four "Side orders: A smorgasbord of treats from assorted arthropod taxa" discusses preparing a variety of insects as well as the non-insect arthropod groups of centipedes, spiders, and scorpions, probably my least desired items for the table. The book contains many marginal notes, called "Bug Bytes," quotes, and other information which give the reader much general information on entomology and entomophagy.

Gordon points out that arthropods are eaten everywhere except for Europe and the United States. Many of these bugs are rich in proteins and are good sources of vitamins, minerals, and fats. Many people feel that entomophagy may be a good alternative to eating so much livestock that require large amounts of the earth's resources to raise. Care should be taken to properly clean and completely cook arthropods to reduce or prevent picking up parasites or disease from the arthropods.

Years ago, I had tried "Gusanos de Maguey," the edible caterpillars of the giant skippers (Hesperiidae, Megathyminae, *Megathymus yuccae)* which are deep fried, canned, and sold in Mexico. At that time, I'm sure my taste for insects had not developed, but as I recall, the larvae tasted a bit oily and really not much to them.

I am especially interested in ants, so I looked closely at Chapter 5, "Ants On (and In) the House." There is a typo on page 44 as the species name for *Formica obscuripes* is misspelled *"ubscuripes."* Also, there is some inconsistency in the quantity of ants needed for the recipes and the units of measurement of them. On page 45, Gordon states that 1/4 cup (200 large-bodied [these are apparently large carpenter ants, *Camponotus*], or 500 small-bodied [probably *Formica obscuripes*]) ants are needed, but on page 48 he states that "1/2 cup (about 80 to 100 individuals) western thatching ants *(Formica obscuripes)* or other large bodied ants" are needed. Anyway, from our trials it appears that 1/4 cup equals about 500 of the thatching ants, so the 1/2 cup requirement would more likely require 1,000 ants. This is an important difference if one is out collecting ants for the recipe.

The two recipes I chose to try involved using ants, as my wife and I prepared "Ant Jemima's Buckwheat-bug Griddlecakes" from page 45 and "Ants in Pants" from page 48. We collected thatch ants of the *Formica rufa* group, which are the same taxonomic group, and thus very similar to *Formica obscuripes* that Gordon suggests. The recipe worked well (although we substituted whole wheat flour for buckwheat flour which was unavailable at our supermarket). The thatch ants gave a bit of a crunchy texture to the griddlecakes and, as promised by the book, yielded a bit of an acidic (vinegar) flavor as we bit into the ant gasters. They were good, and will probably become a regular item at breakfast at future Idaho Entomology Group field trips.

"Ants in Pants" was the other recipe we tried. All my life (so far anyway), I've heard of "chocolate-covered ants", but I've never seen them available. Again, Gordon's recipe is easy to follow. The reader can easily experiment with these as a small amount of melted chocolate mix is dripped onto a flat pan covered with waxed paper. The

size can be adjusted to the individual's need. We made fairly small disks, since we did not have many ants available. We placed three ants on each disk while the chocolate was warm enough for them to stick. Later another layer of chocolate is dripped over the top, covering the ants and forming a sandwich disk. We did find that these candies were easier to remove from the waxed paper and to handle if kept cool (refrigerated). The cook can improvise to the size of chocolate desired and the number and kind of ants. They yielded a great, slightly crunchy snack that was enjoyed by the people we offered them to. We intend to add this recipe to our list of party favorites.

The only ant recipe we did not try was "Amaretto Honeypots." These require the replete workers of the honey ant, *Myrmecocystus*. We did not have any available at the time of this book review. These would be very difficult for the casual gourmet to obtain. While the genus is fairly common and widespread in the western United States and Mexico, finding the nests and then having the time and patience to excavate the repletes (some can be a great distance below the earth surface) make them an unlikely candidate to be found in common use.

Upon seeing the illustration of the label for "Hotliz tequila-flavored Candy" containing the "genuine worm," I'm reminded of a couple of points should make about this popular subject: 1) the "worm" is a Lepidoptera larva and 2) it is found in mescal, not in tequila. Tequila is distilled from the fermented liquid of *Agave tequilana*. Mescal, however is fermented from a different species of *Agave* and the "worm" is actually the larva of the Lepidoptera *(Megathymus yuccae)* mentioned earlier. It is interesting to note that Gordon does not mention "eating the worm," a common pastime in many bars and Mexican restaurants in the United States. This maybe the arthropod food item with the largest U.S. consumption—at least considering that they are uncooked and eaten by choice.

Gordon's puns are pretty good; for example he has sections titled: "Bugs in a Rug," "Pest-o," "Ant Jemima's Buckwheat-Bug Griddlecakes," "Alpha-Bait soup," etc. He gets extra credit points for presentation also; the photo displays of his dishes are a feast for the eyes as well.

An index to arthropod taxa used and recipes included would have been a very useful addition to the book. Otherwise, I recommend it as a good general reference and cookbook for anyone interested in entomophagy.

I will keep the book and add it to my library for both entomological and domestic (cookbook) reasons. I suggest that others may find it as interesting and useful.

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NORTHWEST SCIENCE

Information for Authors

Scope of Articles

The pages of *Northwest Science* are open to original and fundamental research in the basic and applied biological and social sciences. All submissions are refereed, usually by two reviewers. Papers are welcome from authors outside of the Pacific Northwest, but at least one author of any paper considered for publication must be a member of the Northwest Scientific Association. The preferred article length for papers published in *Northwest Science* is 20 journal pages or less; authors must contact the Editor in advance before submitting longer papers.

Northwest Science Forum: This section gives readers an opportunity to address scientific issues in a more participatory fashion. The Forum will publish short articles, opinion pieces, and letters relevant to science and natural resource issues in the Pacific Northwest. Responses to previously published articles are particularly encouraged in order to foster an ongoing discussion. Readers are urged to be creative, articulate, and passionate in this section. The Forum will not be peer-reviewed in order to expedite publication. The editor reserves the right to edit manuscripts for grammar and clarity.

Northwest Science Notes: The purpose of "Notes" is to publish short papers (typically less than five journal pages in length). Suggested topics include preliminary results, new methods, significant range extensions, and perhaps taxonomic observations. There is no specific format or content required for articles published here, but all papers will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.

Manuscripts

General Instructions

Submit four copies of the paper (including tables and figures) to the Editor. Manuscripts should be typewritten in 12 point type on 8-1/2 x 11 inch paper, double-spaced throughout (including abstract, acknowledgements, literature cited, tables, and legends for figures); ample margins must also be provided. The format and style of manuscripts should conform to general usage in recent issues and should consist of sections in the following sequence:

- Title Page
- Abstract
- Text (Introduction through Acknowledgements)
- Literature Cited
- Footnotes
- Tables
- Figure Legends
- Figures

Numerals will be used to indicate footnotes unless such usage would be confused with numerical data. In this situation, lowercase letters should be used. Do not break, or hyphenate, words at the ends of lines. Words to be italicized should be typed in italics rather than underlined.

Title Page

The first page of the manuscript should contain:

- Author's name (or names)
- Institutional address from which manuscript emanated, including city, state or province, postal code
- Title of paper
- Running head
- Total number of text figures and tables
- List name, full address, telephone number, fax number, and e-mail address of the individual to whom correspondence should be sent. Use a footnote to indicate a corresponding author other than the senior author. The footnote should read "Author to whom correspondence should be addressed."

Abstract

The purpose of an abstract is to briefly summarize the study so it is quickly accessible to the

general readership of the journal. The abstract, written in complete sentences and not exceeding 250 words, should precede the text on a separate page. Authors are reminded of the diverse disciplines and readership served by the journal. With this in mind, the abstract should have three parts of unequal length. First, the abstract should begin with a statement of the purpose of the study that indicates why the study was undertaken. Next the experimental design or approach should be stated and the results summarized. The abstract should end with a sentence or two on the larger significance of the research. Authors are strongly encouraged to give the abstract proper attention.

Text

Literature citations within the manuscript text should contain the author's name and year of publication, using formats A and B.

- Format A:

  ...studied by Jones (1978)...

  ...studied by Smith and Brown (1979)...

  ...studied by Smith et al. (1980)... (if more than two authors in a citation)

- Format B:

  ...was previously investigated (Smith 1965, Jones 1971, Harris 1982)...

  ...results of other investigations (Smith 1966, 1970; Jones 1973; Brown 1974)...

Numbers from one to nine will be spelled out, while Arabic numerals will be used for numbers 10 and larger. Exceptions to this rule are: 1) a series of "mixed" numbers (e.g., 14 elk, 35 deer, 2 bobcats, and 1 bear); 2) when the number immediately precedes an abbreviation for a standard unit of measure (e.g., 3 g, 18 mm, 300 m^2). Arabic numerals will also be used for dates, times, page numbers, and percentages.

Authors are requested to use the International System of Units (SI). English equivalents may be added parenthetically. Use the 24-hour clock (0600 and 2230) and continental dating (17 November 1986). Use leading zeroes with all numbers <1 (e.g., 0.12), including probability values with "P" capitalized and in italic (e.g., $P \leq 0.001$).

On first mention, a species should be designated by common name followed by systematic binomial (italicized). Common names for species should not be capitalized except when derived from a proper name. Thus, "mountain hemlock" or "white-crowned sparrow," but "Douglas-fir" or "Clark's nutcracker." In general, authors should follow "conventions" for their respective disciplines (e.g., botany, ornithology). Consult with the Council of Biology Editors *CBE Style Manual*, 4th ed., for general information on manuscript preparation.

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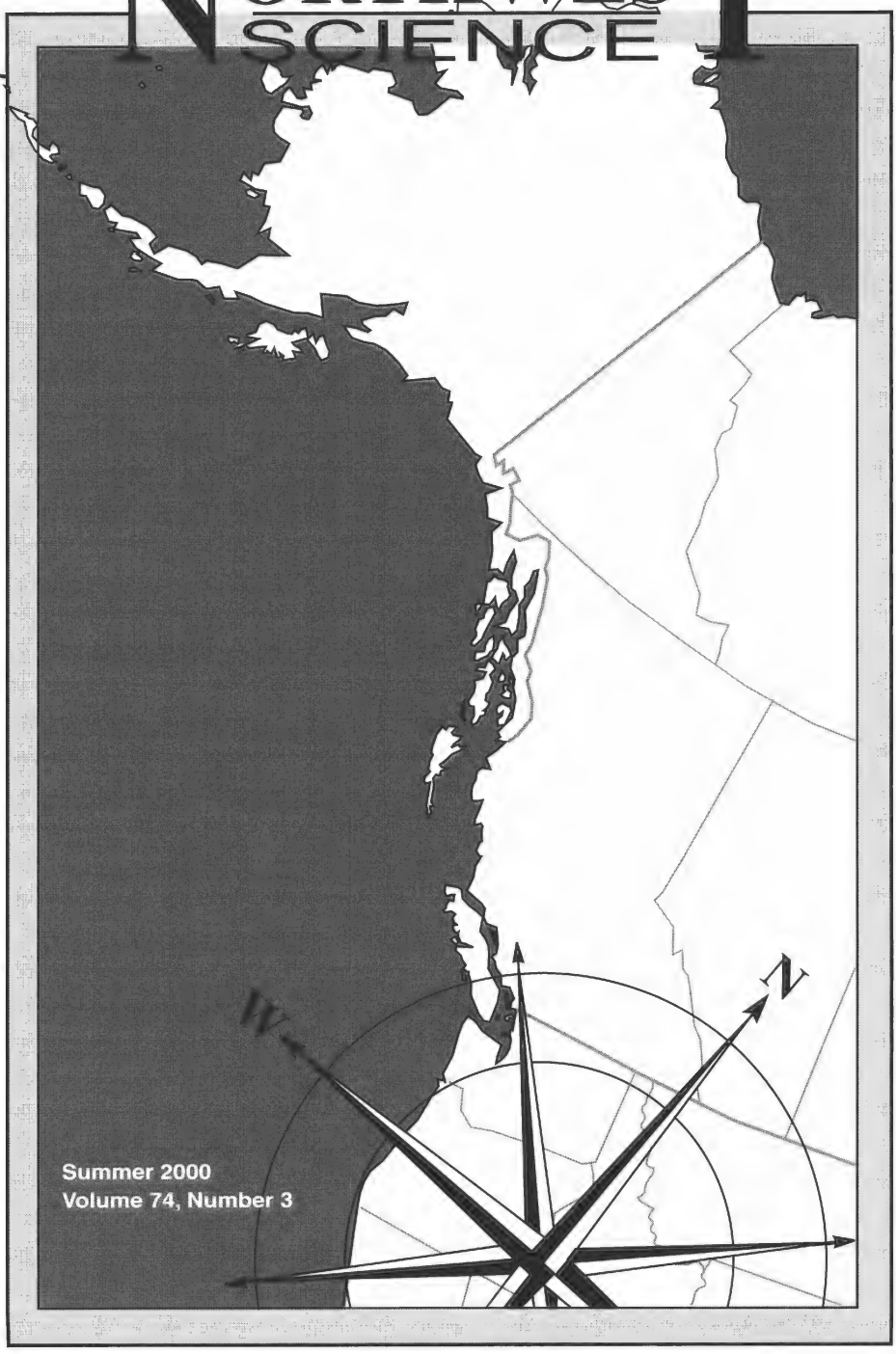

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Resting and Denning Sites of American Martens in Northeastern Oregon

Abstract

Resting and denning sites of the American marten (*Martes americana*) are important habitat components because they provide protection from predators, inclement weather, and thermal stress. Resting sites (n = 1184) used by 35 radiocollared martens were in trees with natural platforms (43%), in trees with cavities (23%), subnivean (under snow) (23%), in hollow logs or slash piles (7%), and underground (3%). Thirty natal and post-natal dens were in trees with cavities (40%), in hollow logs (37%), underground (17%), and in slash piles (6%). Resting and denning sites in cavities and hollow logs were typically large-diameter structures with extensive heartwood decay that had created hollow chambers. The majority of platforms used as resting sites were formed by broom rust (*Chrysomyxa arctostaphyli* and *Melampsorella caryophyllacearum*) and dwarf mistletoe (*Arceuthobium* spp.). Incorporating habitat needs of martens in forest management practices by retaining coarse woody debris and trees with brooms is one component necessary for maintaining viable populations of the species.

Introduction

Resting and denning sites are key attributes of American marten (*Martes americana*) habitat that contribute to meeting behavioral and physiological requirements of the species. Martens are highly selective of their microenvironments for thermal cover, protection from predators and inclement weather (Buskirk et al. 1989, Raphael and Jones 1997), and access to subnivean foraging sites (Buskirk and Ruggiero 1994). The thermal relationship of the marten to its environment is a tenuous one, particularly in winter. Because the energetic cost of foraging and resting above the snow surface is high, martens exhibit patterns of habitat selection that are keyed to weather variables (Buskirk et al. 1987). Selection of denning and resting sites may differ in different forest environments (Raphael and Jones 1997) in response to variability in predators, prey, climate, and availability of habitats. The overall objective of the study was to determine the habitat structures that are important to martens so managers can provide appropriate habitat. In this paper we describe the resting and denning sites of the American marten in northeastern Oregon, which has not been previously investigated.

Study Area

The study area encompassed about 400 km^2 in the Blue Mountains in northeastern Oregon. A portion of the study area contained about 53 km^2 of predominantly unmanaged continuous forest, while the surrounding portion was extensively fragmented by timber harvesting and roaded. The landscape was a mosaic of stands in four forest types (Johnson and Hall 1990): lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), grand fir (*Abies grandis*), and Douglas-fir (*Pseudotsuga menziesii*). Topography of the study area consisted of moderately steep mountains dissected by drainages. Permanent water in the form of springs and streams was abundant. The elevation ranged from 1320 to 1980 m.

Daytime maxima in summer normally exceeded 24°C, and winter low temperatures were typically below freezing, with extremes of -15°C being common. Annual precipitation averaged 78 cm with about 60% falling as snow depending on the elevation. At the highest elevation, snow was present from November through April each year with maximum depths of 1.5 m. At the lowest elevation, snow was present from December until March, with maximum depths of 0.5 m.

Carnivores that commonly occurred in the study area and were known to prey on martens included coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Bull, unpublished data). No evidence of fishers (*Martes pennanti*) was found, and mountain lions (*Felis concolor*) were uncommon. Potential raptorial predators of martens in the study area included the northern goshawk (*Accipiter gentilis*) and great horned owl (*Bubo virginianus*).

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Methods

The study began in December 1993 and ended in October 1997. Martens were captured in cage-type steel live traps (model 205, Tomahawk Live-Trap Co., Tomahawk, Wisconsin) with attached plywood boxes. During the winter, we used snowmobiles to check traps daily. Captured martens were immobilized (Bull et al. 1996) and fitted with a radiocollar (Holohil Inc., Ontario, Canada). Transmitters on females and males weighed 28 g (4% of average body weight) and 35 g (3% of average body weight), respectively.

Radiocollared martens were located on the ground visually, an average of once a week in the winter and twice a week in the summer. The marten or the specific structure (such as tree, log, or underground site) that the marten was using was located to obtain microhabitat data. Characteristics of the transmitter signal were used to determine if the marten was resting or traveling (Raphael and Jones 1997). We believe our presence did not influence behavior of martens in rest sites, because they rarely left a rest site when we approached. If the marten was moving, we followed it until we thought we were within 100 m of the animal, based on the strength of its signal (i.e., the number of MHz above the marten's radio frequency). Based on sightings of traveling martens, we determined we were within 100 m of a marten if we could detect the signal 0.020 MHz above the actual transmitter frequency. For each marten, we recorded date, time, activity, behavior, snow depth, if the marten was actually seen, and characteristics of the rest site.

If a marten was in a rest site, it was classified as a cavity in a tree, a natural platform or branch in a tree, underground, subnivean, slash pile, or a hollow chamber in a log. Each site was assigned an individual number, and subsequent uses by the same marten were classified as re-use. If the rest site was in a standing tree, the species, dbh, height, condition, canopy depth (percentage of the bole that contained live or dead branches), and type of platform or cavity were recorded. Tree condition was classified as living or dead. If the rest site was in a hollow chamber in a log, species, large-end diameter, and length were recorded. If the rest site was in a slash pile, the length, width, and height of the pile were recorded, in addition to the number of logs in the pile and the average diameter of the logs.

Rest sites in platforms were classified as broom rust, mistletoe broom, lichen nest, branches, or unknown. We climbed to 26 platforms to determine type of platform and measure the size of the platform, size of inner nest, and canopy closure (measured with a densiometer).

To locate dens, we located adult females an average of three times each week from the time of parturition until kits were independent. Definitions of natal and post-natal (i.e., maternal) dens are consistent with those by Ruggiero et al. (1998). Although the presence of offspring was not always confirmed, repeated use of a given site in April and May signified a den. Non-denning animals do not typically re-use sites for long periods (Raphael and Jones 1997). Natal dens (supposed parturition sites) were dens where females were first detected and were repeatedly used by an adult female in April or May. Post-natal dens were sites to which females moved the kits after leaving the natal den. Natal dens were more likely to be detected because females were more sedentary here than after kits were moved to post-natal dens. We recorded the same characteristics for natal and post-natal dens as rest sites.

Marten behavior (resting versus traveling) and use of rest sites were compared by month using chi-square analyses. The relationship between snow depth and behavior and between snow depth and use of rest sites was determined by using an analysis of variance and a protected least significant differences test (Snedecor and Cochran 1980).

Results

Rest Sites

Thirty-five martens were located a total of 2353 times between December 1993 and October 1997. Martens were in rest sites at 66% of the locations and traveling at 34%; martens were located only during daylight hours. There was a significant difference in diurnal behavior by month (X^2 = 347.14, 11 df, $P = 0.01$) (Figure 1) and by snow depth (LSD = 4.35, $P < 0.05$). Most of the martens were in rest sites during winter when snow was on the ground, but most of the martens were traveling during summer.

Of 1184 locations at rest sites, 43% were in trees with platforms, 23% in trees with cavities, 23% subnivean, 7% in hollow logs or slash piles, and 3% underground (Table 1). Twenty percent

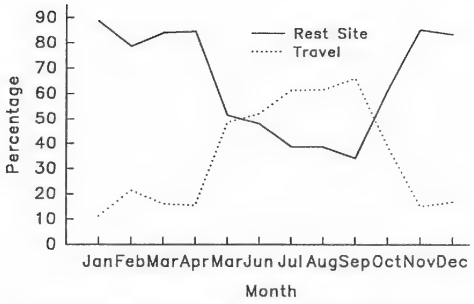

Figure 1. Percentage of martens located during daylight hours that were in rest sites and those traveling by month in northeastern Oregon, 1993-97.

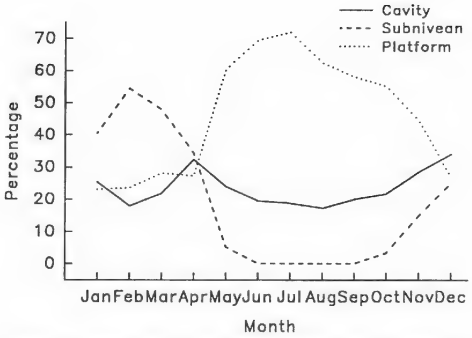

Figure 2. Marten use of three types of rest sites by month in northeastern Oregon, 1993-97.

TABLE 1. Structures (%) used as resting and denning sites by American martens in northeastern Oregon, 1993-97.

	Resting Sites	Natal Dens	Post-Natal Dens
Platforms	43		
Cavities	23	73	21
Subnivean	23		
Hollow log	6		58
Underground	3	27	10
Slash piles	1		10
Sample size	1184	11	19

TABLE 2. Tree species (%) and tree characteristic means (SD) of three types of resting sites used by American martens in northeastern Oregon, 1993-97.

Characteristic	Platforms	Cavities	Hollow Logs
Tree species			
Grand fir	11	58	58
Western larch	10	32	17
Engelmann spruce	43	5	7
Subalpine fir	25	3	8
Douglas-fir	9	1	3
Lodgepole pine	1		
Ponderosa pine	1	1	7
Tree dbh (cm)	51.7 (20.94)	78.9 (21.22)	66.1 (18.38)
Tree height (m)	26.4 (7.85)	21.2 (9.85)	19.7 (10.68)
Marten height (m)	12.6 (5.99)	11.2 (6.74)	
Canopy depth (%)	89.1 (18.62)	52.4 (39.63)	
Sample size	517	271	67

of the rest sites were used more than once, and not always by the same individual. We saw the marten in 24% of the rest sites, so we are confident we identified the correct sites. A significant difference was found between type of rest site used and month ($X^2 = 428.74$, 55 df, $P < 0.01$) (Figure 2) and between rest site use and snow depth (LSD = 14.35, $P < 0.05$). Subnivean sites were different from all other types of rest sites because they had the deepest snow ($\bar{x} = 101$ cm), as one would expect.

Trees with platforms were the dominant rest sites from May until October (Figure 2). We saw platforms in 84% of the trees used by martens; the marten was on a branch in 6%; and a platform was impossible to detect because of dense branches in 9%, but we assumed a platform was present in these trees. The misshapen branches (witches' brooms) used by martens were caused by rust fungi or dwarf mistletoes. In Engelmann spruce (*Picea engelmanni*) and the true firs where 79% of the platforms occurred, broom rust created the platforms (*Chrysomyxa arctostaphyli* in spruce and *Melampsorella caryophyllacearum* in subalpine fir). Dwarf mistletoe (*Arceuthobium* spp.) caused the brooms in western larch (*Larix occidentalis*), Douglas-fir, lodgepole pine, and ponderosa pine (*Pinus ponderosa*) where 21% of the platforms occurred. Most of the trees (92%) were living, and the average dbh was 52 cm (Table 2). Trees typically had branches along the entire length of the bole.

Of 26 trees that we climbed which contained platforms used by martens, 50% were platforms caused by broom rust, 19% were caused by dwarf mistletoe, 19% were constructed nests made of lichen (*Bryoria* spp.), and 12% were in a tree fork or on a group of branches. Twenty of the 26

platforms had 100% canopy closure over the platforms, thus providing the martens with dense cover and protection from weather and avian predators. Ninety-two percent of the platforms contained a smaller nest where the marten appeared to spend time; 85% of these nests had been constructed, presumably by squirrels or martens. Of the 24 platforms with nests, lichens were the dominant component at 75% of the platforms, grass at 8%, sticks at 8%, and needles at 8%. Lichen nests averaged 24 cm long, 22 cm wide, and 15 cm deep and were constructed on one or several branches.

Of the 13 platforms formed by broom rust, all were in Engelmann spruce except one in a subalpine fir. Outside broom dimensions averaged 57 cm long, 67 cm wide, and 78 cm deep. All brooms consisted of branches <1 cm in diameter, and many formed a dense structure used as a rest site.

Mistletoe formed five brooms used by martens, three of which were in western larch and two in Douglas-fir. These brooms tended to be flatter on top than brooms formed by broom rust. Outside broom dimensions averaged 54 cm long, 61 cm wide, and 37 cm deep.

Trees with cavities were used as rest sites all year, although April and December had the greatest use (Figure 2). The majority of cavities were in grand fir and western larch (Table 2). Sixty-seven percent of the trees were dead, and the rest living. Most of the trees with cavities used by martens were hollow, based on the presence of fruiting bodies of Indian paint fungus (*Echinodontium tinctorium*) on grand fir, and of brown trunk rot (*Fomitopsis officinalis*) and red ring rot (*Phellinus pini*) on western larch. Martens entered these hollow trees through broken tops, holes excavated by pileated woodpeckers (*Dryocopus pileatus*), or through natural cavities usually created when a branch broke off. Cavities occurred in large-diameter trees, although not necessarily tall (Table 2) because an average of 30% of the bole was broken off.

During the winter martens spent most of their time in subnivean rest sites (Figure 2), in the open spaces created when horizontal structures (usually logs) kept the snow off the ground. Some of the subnivean sites had extensive systems of tunnels under logs where the martens could travel for >30 m, based on observations at these sites when the snow was melting. The martens presumably both hunted and rested under the snow. Use of these sites tapered off in late winter or early spring even though snow remained.

We revisited 93 subnivean rest sites after the snow had melted and found an accumulation of logs (42%), a hollow log (20%), a single large log (>60 cm in diameter) (16%), an underground site (13%), or a slash pile of logs (9%). Most of the underground sites were accessed through tunnels 5-15 cm in diameter in the soil. At least 75% of the subnivean rest sites had evidence of red squirrel (*Tamiasciurus hudsonicus*) middens with either tracks or cone scales.

During the snow-free months, hollow logs comprised 6% of the rest sites, but 20% of the revisited subnivean rest sites were also hollow logs. The majority of hollow logs were grand fir and western larch (Table 2), no doubt because of the heartwood decay responsible for the hollow chambers.

Slash piles left from harvesting or road building comprised 1% of the snow-free rest sites, and 9% of the subnivean rest sites. The mean dimensions of the piles were 12 m long, 7 m wide, and 3 m high. The mean number of logs in the piles was 62, with an average diameter of 28 cm.

Thirty-eight rest sites were underground: 53% were in tunnels, 37% in rocks, and 10% in root wads. The underground tunnels appeared to have been excavated. The rest sites in rocks were in talus, boulder fields, or isolated clusters of rocks.

Dens

Eleven natal and 19 post-natal dens were located for 8 females (11 female-years) during 1994-97. Natal dens were either in a cavity or underground, while post-natal dens also included hollow logs and slash piles (Table 1). The trees with cavities used as dens were grand fir (84%), western larch (8%), and subalpine fir (8%); a third of these trees were alive. We believe all of these cavities consisted of hollow chambers because a woodpecker cavity would not be large enough to contain the kits. The dens in grand fir and western larch were entered through pileated woodpecker holes or broken off tops. The den in the subalpine fir was entered through a natural cavity in the base of the dead tree and appeared to go underground. The trees averaged 83 cm dbh and 23 m tall. Most of the trees had branches along the majority of the bole.

Hollow logs used for dens were grand fir (55%), western larch (27%), Engelmann spruce (9%), and subalpine fir (9%). The logs averaged 73 cm in diameter at the large end and 24 m long. All the logs had hollow chambers, and the five that could be measured were 20-25 cm in diameter inside. Two slash piles served as post-natal dens. One pile of five logs was on the edge of a closed road and was 10 m long, 2 m wide, and 1 m high. The second pile contained more than 200 logs and was 16 m long, 10 m wide, and 6 m high.

Five of the dens were underground. One natal den was in an underground system of rock fissures that extended more than 7 m underground into a complex structure of cracks and fissures. Another den was in a boulder field. Root wads served as the entrance to two dens, and squirrel middens appeared to be the entrance hole to another den.

Discussion

The reduced diurnal activity of martens in winter that we observed has been observed by other researchers as well (Buskirk (1983), Drew and Bissonette (1997), and Zielinski et al. (1983). This reduced activity could be a behavioral strategy to reduce their vulnerability to predation due to their increased visibility with snow contrasting against their dark pelage. Thermal stress is most significant in winter, and the dietary shift we observed to larger prey items (Bull, unpublished data) could have resulted in the martens' spending less time foraging or synchronizing their periods of activity with that of their prey.

Obvious patterns of resting site use emerged over the course of the study. As soon as deep snow accumulated, martens rested in subnivean spaces formed by coarse woody debris. Use of subnivean resting sites has been well documented in other areas (Sherburne and Bissonette 1994, Buskirk and Ruggiero 1994, Buskirk and Powell 1994, Chapin et al. 1997). These subnivean sites provided good thermal regulation because the ground was often not frozen under these sites (based on excavations at several sites); whereas, the ambient air temperature could be as cold as -15°C. In addition, most subnivean sites were inaccessible to predators, and many were occupied by red squirrels at their middens; red squirrels were a prey item in the winter in our area. The access to many of these resting sites were tunnels through the snow which appeared to have been made by the squirrels. This association between martens and squirrel middens has also been reported by Buskirk (1983), Sherburne (1992), and Sherburne and Bissonette (1994). Use of subnivean sites tapered off in April before snow disappeared, which suggested that melting snow may have saturated the ground making these sites undesirable.

Cavity use peaked in April and from November to December. During these time periods the weather was cold with frequent precipitation, making use of platforms undesirable. Snow accumulations were often not sufficient by December to form subnivean resting sites, and the ground was likely saturated in April. Cavities provided dry, insulated sites that were inaccessible to their predators. We believe the majority of cavities used in our study area were hollow chambers based on a previous study in which 60 trees with similar characteristics were climbed; 95% were found to be hollow (Bull et al. 1992). Typically, only large-diameter trees contain a hollow chamber large enough for a marten to use because the chamber forms only when the former heartwood has decayed and slumped downward (Bull et al. 1997). The high use of living trees occurred because hollow chambers caused by heartrot fungi are created while the tree is still alive (Bull et al. 1997). This decay process can take decades to develop, and trees may be several hundred years old. Typically, these hollow trees occur in forest stands of grand fir in late-successional stages, which now occupy only about 3% of the landscape in northeastern Oregon (Bull et al. 1997). The use of cavities in large-diameter trees that we observed has been reported by Steventon and Major (1982), Spencer (1987), Martin and Barrett (1991), Buskirk and Ruggiero (1994), and Raphael and Jones (1997); however, these studies did not specify if the resting sites were vacated woodpecker cavities or hollow chambers.

Our study was unique in observing a dominant use of platforms as resting sites during the summer. Only Campbell (1979) and Buskirk et al. (1987) reported use of witches' brooms by martens, although other studies (Martin and Barrett 1991, Raphael and Jones 1997) reported use of live trees which may have contained brooms not visible to observers. The brooms formed by broom rust in spruce and firs in our study presented dense spheres of branches that would be impenetrable

to predators. Brooms also are readily used by squirrels as resting sites (Parks et al. 1999), so they may have provided martens with a source of prey as well as a secure resting site.

Dens differed from rest sites in being more secure. Natal dens were in structures (hollow trees and underground) that were dry, insulated, and inaccessible to any predator other than another marten. Post-natal dens were less secure than natal dens, presumably to accommodate for movement of kits; nevertheless, the majority were still inaccessible to most mammalian predators. In one situation a bear had ripped open a portion of a log that contained kits. The common feature we observed among natal and post-natal dens was the large diameter of the structure. Buskirk and Ruggiero (1994) reviewed 14 studies and provided a summary of den structures: 70% of dens were in trees, logs, and rocks, and the dens in trees were always in large structures associated with late-successional forests. Ruggiero et al. (1998) described 18 natal dens and 97 post-natal dens in Wyoming. Large-diameter trees were a critical feature in dens in Washington and Oregon (Raphael and Jones 1997).

The findings in our study can be used by managers to retain the appropriate structures to provide martens with rest sites and dens. Large-diameter hollow trees and logs, accumulations of coarse woody debris, and trees with brooms provided important habitat for resting sites. The silvicultural practices of removing trees with brooms, removing hollow trees, and reducing fuels (coarse woody debris) to lower the risk of or damage by wildfire may negatively alter marten habitat. Incorporating the habitat needs of martens into forest management plans can ensure the maintenance of viable populations across landscapes.

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Seasonal and Sexual Differences in American Marten Diet in Northeastern Oregon

Abstract

Information on the diet of the American marten (*Martes americana*) is vital to understanding habitat requirements of populations of this species. The frequency of occurrence of prey items found in 1014 scat samples associated with 31 radiocollared American martens in northeastern Oregon included: 62.7% vole-sized prey, 28.2% squirrel-sized prey, 22.4% insects, 19.5% birds, 13.3% plant material, and 2.4% lagomorphs. A significantly higher proportion of voles (*Microtus* spp.), southern red-backed voles (*Clethrionomys gapperi*), and chipmunks (*Tamias* spp.) were found in the summer diet compared with the winter, and a higher proportion of northern flying squirrels (*Glaucomys sabrinus*), unidentified squirrels, bushy-tailed woodrats (*Neotoma cinerea*), and mountain cottontails (*Sylvilagus nuttallii*) were found in the winter diet compared with summer. Insects and plant remains represented a higher proportion of the diet in summer than winter. Females preyed on a higher proportion of shrews (*Sorex* spp.) and chipmunks, while males preyed on a higher proportion of southern red-backed voles.

Introduction

The American marten (*Martes americana*) is considered to be a habitat specialist in the western U.S. (Buskirk and Powell 1994, Raphael and Jones 1997), but studies of its food habits indicate that martens are generalist predators, feeding on a variety of small mammals, birds, insects, fish, carrion, and vegetation (Martin 1994). In theory, a generalist predator will switch to alternative prey species when preferred prey are not readily available and will select food items that result in energy returns equal to or higher than the energy expended capturing and consuming that food (Ben-David et al. 1997).

Martin (1994) reviewed 22 studies reporting marten diet. Voles were reported as important food items across the range of the marten and were dominant in half the diets; only 2 of the studies reviewed did not find voles to represent at least 10% of the diet. Seasonally abundant foods (e.g., insects and fruit) were eaten when available in Idaho (Koehler and Hornocker 1977). In Alaska, voles and fruit were important food items during the autumn but declined in importance over the winter (Buskirk and MacDonald 1984). In California, vole representation in the diet decreased in late winter and spring diet, while ground squirrel and chipmunk representation in the diet increased in the summer (Zielinski et al. 1983). In southeast Alaska, use of salmon and voles changed seasonally (Ben-David et al. 1997)

Intersexual differences in marten diet have been reported in relatively few studies. On Vancouver Island in British Columbia, female martens consumed more small mammal and small bird prey than did males, but there was extensive dietary overlap between the sexes (Nagorsen et al. 1989). In contrast, Thompson and Colgan (1990) found no sexual differences in diet in Ontario.

Marten food habits differ substantially in different geographic areas (Martin 1994). Consequently, research findings in one area may not be applicable in other habitats or localities. The National Forest Management Act of 1976 (USDA 1978) mandated that viable populations of all native species be maintained on federal lands. On National Forests, managers are required to provide adequate habitat to sustain viable populations of martens. Knowledge of marten diet is critical for effectively managing habitat for martens and their prey. My objectives in this study were to determine the seasonal and sexual differences in diets of martens in northeastern Oregon.

Methods

The study area encompassed about 400 km^2 in the Blue Mountains in northeastern Oregon. The landscape was a mosaic of uneven-aged stands in four forest types (Johnson and Hall 1990): lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), grand fir (*Abies grandis*), and Douglas-fir (*Pseudotsuga menziesii*). Approximately

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80% of the study area had been managed with partial overstory removals, regeneration cuts, and selection harvests. Topography consisted of moderately steep mountains dissected by drainages with permanent water in the form of springs and streams. The elevation ranged from 1320 to 1980 m.

Daytime maxima in summer normally exceeded 24°C, and winter low temperatures were typically below freezing with extremes of -15°C being common. Annual precipitation averaged 78 cm with about 60% falling as snow. At the highest elevations, snow was present from late October through April each year with maximum depths of 1.5 m. At the lowest elevation, snow was present from December until March, with maximum depths of 0.5 m.

I determined diet from direct observation of martens with prey, from prey remains, and from scats collected at rest sites and dens from January 1994 until October 1997. Thirty-one radiocollared martens (12 females and 19 males) were located on the ground visually, an average of once per week in the winter and twice per week in the summer. The marten or the specific structure (e.g., tree, log, underground site) that the marten was using was located. When a marten was located, I attempted to see the animal and record any foraging information. The immediate vicinity (within 30-m radius) was searched for scats and prey remains. Many of the marten locations in the winter were at subnivean rest sites, which were revisited immediately after the snow melted to search for scats and prey remains. Prey remains and scats were put in plastic bags and labeled with the date, number of scats, age of scat (fresh or old), and identifying number of the marten. Fresh scats were determined to have been deposited within a week based on a dark color and moist condition; old scats had been deposited longer than a week. Individual scats could not be separated at some dens and rest sites with latrines. Rest sites used by more than one marten were labeled with both marten numbers because I could not be certain which had deposited the scat; scats collected at these sites were excluded in the comparisons between sexes. When old scats were collected, they were classified as "winter," "summer," or "unknown" based on their appearance and when they were collected. Summer scats were those that I determined had been deposited between 18 April and 14 October; winter scats were deposited between 15 October and 17 April of each year. These dates were selected because temperatures were below freezing and snow started falling by mid-October; by mid-April, snow was melting and temperatures were typically above freezing. Scats and prey remains were frozen until they were analyzed.

Individual scats were placed in a nylon bag with a waterproof label, soaked for 10-12 hours in a mild bleach and detergent solution, and dried. Each scat sample was separated into three components: guard hairs; bones and teeth; and nondiagnostic material (mainly gray underfur). Feathers, insects, plant remains, and other materials were removed and identified if possible. Feathers usually did not survive the digestive process well enough to be identified to species, so feathers in a scat were recorded as bird remains. Fruits were identified to species by using a reference collection of berries collected in the study area. Insects were identified to the lowest taxon possible; very small fragments of insects found in scats with bird remains were considered secondary prey from the bird and not counted.

Identification of small prey (e.g., voles) was based on skull fragments, lower jaws, and teeth. After the bones were identified, guard hairs were identified using a compound microscope. Detecting the presence of larger prey often depended solely on identification of guard hairs because of the frequent lack of diagnostic bones or teeth. It is likely this method over estimated the larger prey items because remains from the same individual prey could be contained in more than one scat. This overestimation of larger prey items plus the unknown bird species consumed made a calculation of biomass inappropriate. Sources used for identification included Stains (1958), Hoffman and Pattie (1968), Glass (1973), Brunner and Coman (1974), Moore et al. (1974), Zielinski (1986), Thompson et al. (1987), and Jones and Manning (1992).

Frequency of occurrence for all prey items was determined. For each prey species that occurred in >10 scat samples, a chi-square analysis (Snedecor and Cochran 1980) was used to compare the frequency of occurrence between sexes and between summer and winter. A significance level of 0.05 was used for these tests.

Results

Prey items representing 17 mammal species, birds, fish, 6 species of fruits, and insects were identified

in 1014 scat samples (Table 1). By frequency of occurrence, the majority (63%) of the scat samples contained vole-sized prey (primarily *Microtus* spp. and southern red-backed voles), and 28% squirrel-sized prey. Seven mammal species were not equally represented in the scats in the summer and winter. A significantly higher proportion of *Microtus* ($X^2 = 167.20$, 1 df, $P < 0.001$), southern red-backed voles ($X^2 = 12.65$, 1 df, $P < 0.001$), and chipmunks ($X^2 = 24.09$, 1 df, $P < 0.001$) were found in the summer, whereas, a higher proportion of northern flying squirrels ($X^2 = 7.754$, 1 df, $P = 0.005$), unidentified squirrels ($X^2 = 21.536$, 1 df, $P < 0.001$), bushy-tailed woodrats ($X^2 = 4.776$,

TABLE 1. Frequency of occurrence (%) of prey items found in 1014 scat samples from 31 radiocollared American martens during summer (18 April-14 October) and winter (15 October-17 April) in northeastern Oregon, 1993-1997.

Prey item	Summer	Winter	All year
Mammals			
Vole (*Microtus* spp.)	50.2	9.6	27.4
Southern red-backed vole (*Clethrionomys gapperi*)	30.3	19.4	24.6
Unknown vole	12.4	11.0	12.7
Deer mouse (*Peromyscus maniculatus*)	10.4	8.4	7.8
Unknown shrew (*Sorex* spp.)	4.9	6.4	4.7
Unknown chipmunk (*Tamias* spp.)	6.5	0.6	2.7
Northern pocket gopher (*Thomomys talpoides*)	3.9	2.0	2.6
Coast mole (*Scapanus orarius*)	—	0.4	0.2
Bat (*Myotis* spp.)	—	0.2	0.1
Total vole-sized prey	83.1	46.1	62.7
Unknown squirrel	11.1	24.4	17.3
Northern flying squirrel (*Glaucomys sabrinus*)	2.6	7.2	4.3
Red squirrel (*Tamiasciurus hudsonicus*)	2. 9	3.0	3.3
Bushy-tailed woodrat (*Neotoma cinerea*)	1.3	4.0	2.5
Unknown ground squirrel (*Spermophilus* spp.)	—	0.2	0.1
Weasel (*Mustela* spp.)	0.7	1.0	0.8
Total squirrel-sized prey	18.6	39.7	28.2
Snowshoe hare (*Lepus americanus*)	2.2	1.2	1.4
Mountain cottontail (*Sylvilagus nuttallii*)	—	1.8	0.9
Unknown lagomorph	—	—	0.1
Total hares and rabbits	2.2	3.0	2.4
Unknown cervid	—	2.6	2.0
Common porcupine (*Erethizon dorsatum*)	0.3	—	0.2
Birds	15.3	19.8	19.5
Egg shell	0.7	—	0.2
Fish	—	0.4	0.2
Insects (total)	31.3	15.6	22.4
Wasps	24.9	7.6	15.6
Ants	4.2	3.8	3.9
Other insects	11.1	6.0	7.8
Plants (total)	27.5	5.2	13.3
Big huckleberry (*Vaccinium membranaceum*)	5.4	0.2	2.6
Grouse huckleberry (*V. scoparium*)	3.9	—	1.4
Currant (*Ribes* spp.)	8.4	0.1	3.9
Strawberry (*Fragaria* sp.)	3.0	0.2	1.1
Rose (*Rosa* sp.)	0.3	0.6	0.5
Raspberry (*Rubus idaeus*)	0.9	—	0.3
Wood fibers, lichen, grass	7.8	4.0	4.8
Number of scat samples	307	501	1014

1 df, $P = 0.029$), and mountain cottontails ($X^2 = 5.577$, 1 df, $P = 0.018$) were found in the winter (Table 1).

Seventy-four percent of the scat samples could be attributed to either male or female martens. Significant differences occurred between males and females in the occurrence of shrews ($X^2 = 7.48$, 1 df, $P = 0.006$), chipmunks ($X^2 = 4.57$, 1 df, $P = 0.033$), and southern red-backed voles ($X^2 = 10.185$, 1 df, $P < 0.001$) in scats. Females preyed on a higher proportion of shrews and chipmunks than males, whereas males took a higher proportion of southern red-backed voles. Birds comprised 19.5% of the prey items in the scats, though species could not be determined from scat remains (Table 1). Eggs shells were found in some scats suggesting that nests were raided. No significant differences were detected in the occurrence of birds in scats by sex or by season.

Remains of insects were found in 22% of the scats; the majority were bald-faced hornets or yellowjackets (referred to as wasps collectively). Significant differences were found in the occurrence of insects between summer and winter ($X^2 = 27.77$, $P < 0.001$). Though most of the wasp remains were in scats in the summer, some were found in October, November, and February; martens were observed excavating yellowjacket nests in October and November.

Overall, 13% of marten scats contained plant material. Fruit from big huckleberry, grouse huckleberry, and currant comprised most of the plant material in scats, although grass, lichen, and wood fibers occurred year round in small amounts. Significant differences in frequency of fruits occurred between seasons ($X^2 = 67.99$, $P < 0.001$). As one would expect, the majority of plant material in the form of fruit was available in the summer.

Prey remains of 8 mammalian and 13 avian species were found at dens and rest sites (Table 2) and were biased toward larger prey items and birds, because they were not entirely consumed.

TABLE 2. Species and number of prey remains found at American marten rest sites and dens during summer (18 April-14 October) and winter (15 October-17 April) in northeastern Oregon, 1993-1997. Items are listed in order of importance within each broad taxonomic group.

Prey species	Summer	Winter
Mammals		
Red squirrel (*Tamiasciurus hudsonicus*)	3	12
Snowshoe hare (*Lepus americanus*)	1	3
Northern flying squirrel (*Glaucomys sabrinus*)	2	2
Unknown chipmunk (*Tamias* spp.)	4	
Mountain cottontail (*Sylvilagus nuttallii*)	2	1
Unknown lagomorph	2	
Unknown vole	1	1
Columbian ground squirrel (*Spermophilus columbianus*)	1	
Birds		
Ruffed grouse (*Bonasa umbellus*)	3	5
Common raven (*Corvus corax*)		7
Unknown woodpecker (*Picoides* spp.)	2	1
Pileated woodpecker (*Dryocopus pileatus*)	2	1
American robin (*Turdus migratorius*)	3	
Northern flicker (*Colaptes auratus*)	2	
Swainson's thrush (*Catharus ustulatus*)	1	
Unknown warbler or golden-crowned kinglet (*Regulus satrapa*)	1	
Unknown sparrow	1	
Flammulated owl (*Otus flammeolus*)	1	1
Unknown thrush		1
Brown creeper (*Certhia americana*)		1
Dark-eyed junco (*Junco hyemalis*)		2
Insects		
Yellowjacket (*Vespula* spp.)	2	1
Yellowjacket or bald-faced hornet (*Dolichovespula* sp.)	2	

Identification of the bird species is the primary value of the prey remains. The most abundant bird species were grouse and common ravens, while 5 of the 13 species were cavity nesters. Prey remains of ravens were found only in the winter and only at rest sites of males. Evidence at rest sites based on tracks, feathers, and whitewash suggested that martens killed the ravens at their roost trees. Cavity-nesting birds were likely captured in nest or roost cavities.

Discussion

The diversity of prey taken by martens in this study suggests that this species is functioning as a generalist predator. The shift from taking mostly vole-sized prey in the summer, to taking larger prey (squirrels, woodrats, and lagomorphs) in the winter, may be influenced by the availability and vulnerability of prey, as well as energy constraints. Some mammals hibernate, and others remain under the snow, where they are inaccessible to martens except in subnivean spaces. Red squirrels and snowshoe hares are often on the snow surface, whereas voles rarely are. Taking larger prey items in the winter may be more energy efficient, depending on the search and capture effort involved. Zielinski (In press) suggested that martens increased their foraging efficiency by hunting and eating larger prey in the winter than in the summer. A reduction in their activity in the winter, presumably a result of taking larger prey less frequently, could also be an adaptation to cold stress. Lachowski (1997) also reported that snowshoe hares and red squirrels were more frequently consumed in winter (35%) than in summer (17%) in Maine.

The findings of this study showed similar trends to those reported elsewhere in the interior Northwest. Newby (1951) found that 45% of the food items in marten scats were mammals, 43% were insects, 7% were plant remains, and 4% were birds in Washington; use of insects and plants was higher in summer, whereas use of mammals and birds was higher in winter. In Montana, mammals were found in 93% of the scats, fruits in 29%, insects in 19%, and birds in 12% (Weckwerth and Hawley 1962). Representation in the diet varied by season with the highest use of birds and insects in spring and summer, highest use of fruit during summer and fall, and highest use of mammals in winter (Weckwerth and Hawley 1962). In Idaho, 99% of the scats contained mammals, 12% fruits, 9% insects, and 5% birds (Koehler and Hornocker 1977); use of insects, birds, and plants was highest in summer, whereas use of mammals was highest in winter. Compared with the above studies, the present study typically reported similar use of mammals, higher use of birds, and higher use of insects. Use of plants in the present study was similar to use reported by Koehler and Hornocker (1977), higher than Newby (1951), and lower than Weckwerth and Hawley (1962). Quantification of prey abundance would be required to determine if differences in use of prey among these studies was a function of selection or availability.

Of the literature reviewed by Martin (1994), the present study reported the highest use of insects except for Newby (1951). Yellowjackets are consumed primarily in the western United States where these insects are abundant in forests. Bald-faced hornets typically have aerial nests, and yellowjackets have both aerial nests and nests in woody debris on or in the ground (Borror and Delong 1971). In this study, both types of nests were readily accessible to martens by mid-summer, but only yellowjacket ground nests were available in winter under snow because aerial nests were destroyed by inclement weather in the fall.

This study identified the importance of vole-sized and squirrel-sized mammalian prey, insects, plants, and birds to the American marten in northeastern Oregon. The diversity of prey and the seasonal differences in representation of the food items portrays the opportunistic nature of this species. Consideration of these prey species and their habitat requirements is essential in effectively managing habitat for martens.

Acknowledgements

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White Sturgeon Spawning Areas in the Lower Snake River

Abstract

We documented 17 white sturgeon *Acipenser transmontanus* spawning locations in the Snake River from the mouth to Lower Granite Dam (river km 0 to173). Spawning locations were determined by the collection of fertilized eggs on artificial substrates or in plankton nets. We collected 245 eggs at seven locations in McNary Reservoir, 22 eggs at three locations in Ice Harbor Reservoir, 30 eggs from two locations in Lower Monumental Reservoir, and 464 eggs at five locations in Little Goose Reservoir. All 17 locations were in high water velocity areas and between 1.0 and 7.0 km downstream from a hydroelectric dam. The documentation of spawning areas is important because this habitat is necessary to maintain natural and viable populations.

Introduction

Fishery managers have identified the need for the protection and enhancement of critical white sturgeon *Acipenser transmontanus* habitat (PSMFC 1992). White sturgeon are ancient fish that evolved in and adapted to free-flowing rivers along the Pacific coast of North America. These long-lived fish are susceptible to overfishing (Rieman and Beamesderfer 1990) and environmental perturbations. Dam construction and operation of the Federal Columbia River Power System has adversely affected white sturgeon populations (Beamesderfer et al. 1995, DeVore et al. 1995). Historically, white sturgeon traveled throughout a diverse Columbia River Basin (Bajkov 1951) seeking out and spawning in favorable riverine habitat at peak seasonal conditions (Scott and Crossman 1973).

The need for more information on the habitat requirements of white sturgeon was given top priority in a workshop held in 1983 that ranked research needs for this species (Fickesien et al. 1984). As a result, several studies were undertaken in the lower Columbia River reservoirs during the late 1980's to determine the current status of white sturgeon populations. The studies documented that spawning in the lower Columbia River occurred during the months of April through July primarily within 8 km to 11 km downstream from a dam when water temperatures were between 10° C and 18°(Parsley et al. 1993, McCabe and Tracy 1994). High water velocities (mean column velocities ≥ 0.8 m/s) and solid bottom substrates of bedrock, boulder, or cobble generally characterize white sturgeon spawning habitat (Parsley et al. 1993). Further work by Parsley and Beckman (1994) revealed that the quantity and quality of spawning habitat was influenced by river discharge, reservoir pool elevation, and river channel morphometry. Thus, hydroelectric development in the Columbia River Basin has reduced the availability of riverine habitat needed by white sturgeon for successful spawning (Parsley and Beckman 1994). Currently, most areas of habitat that would be considered suitable for spawning by white sturgeon in the Columbia and Snake rivers are located immediately downstream from hydroelectric dams.

Miller et al. (1995) reports that the status of 25 discrete white sturgeon populations in the Columbia River basin varies. Only 1 population is considered to be stable and abundant and 5 populations are considered to be relatively abundant, but their numbers are probably reduced from historic levels. The remaining populations are considered to be sparse and declining, and the population of white sturgeon in the Kootenai River in northern Idaho has been listed as endangered. Thus, it's imperative to document localized areas that are important to various life stages of these fish so that further perturbations to those habitats can be avoided.

Prior studies of white sturgeon spawning activities did not present detailed information concerning the exact location of spawning sites. This information is critical if the remaining spawning sites are to be protected and possibly enhanced. During earlier work researchers tested gears for collecting white sturgeon eggs from spawning areas. Gears tested included inverted U-shaped

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plankton nets, beam trawls, and artificial substrates (Parsley et al. 1993, McCabe and Beckman 1990). Variants of the artificial substrates described by McCabe and Beckman (1990) are now widely employed by fisheries professionals interested in documenting spawning by several species of sturgeon. They can be left to fish unattended and are relatively inexpensive; thus, many areas can be sampled at a lower cost than with nets or trawls. The objective of our study was to identify specific sites where white sturgeon spawn in the lower Snake River, focusing on dam tailrace areas.

Methods

Sampling for white sturgeon eggs was performed in the lower Snake River from the mouth to river km 173 (Figure 1). River kilometer designations were obtained by converting river miles noted on nautical navigation charts produced by the National Atmospheric and Oceanic Administration. We concentrated sampling effort for white sturgeon eggs downstream from four dams: Ice Harbor (river km 16), Lower Monumental (river km 67), Little Goose (river km 113), and Lower Granite (river km 173). The area downstream from Ice Harbor Dam was sampled in 1993, 1994, and 1995 (Figure 2). Sampling downstream from the Lower Monumental (Figure 3), Little Goose (Figure 4), and Lower Granite (Figure 5) dams was done in 1997 and 1998. Sampling for white sturgeon eggs was performed within the known seasonal spawning period (Parsley et al. 1993, McCabe and Tracy 1994), with sampling beginning when water temperatures approached 12°C and ending when tem-

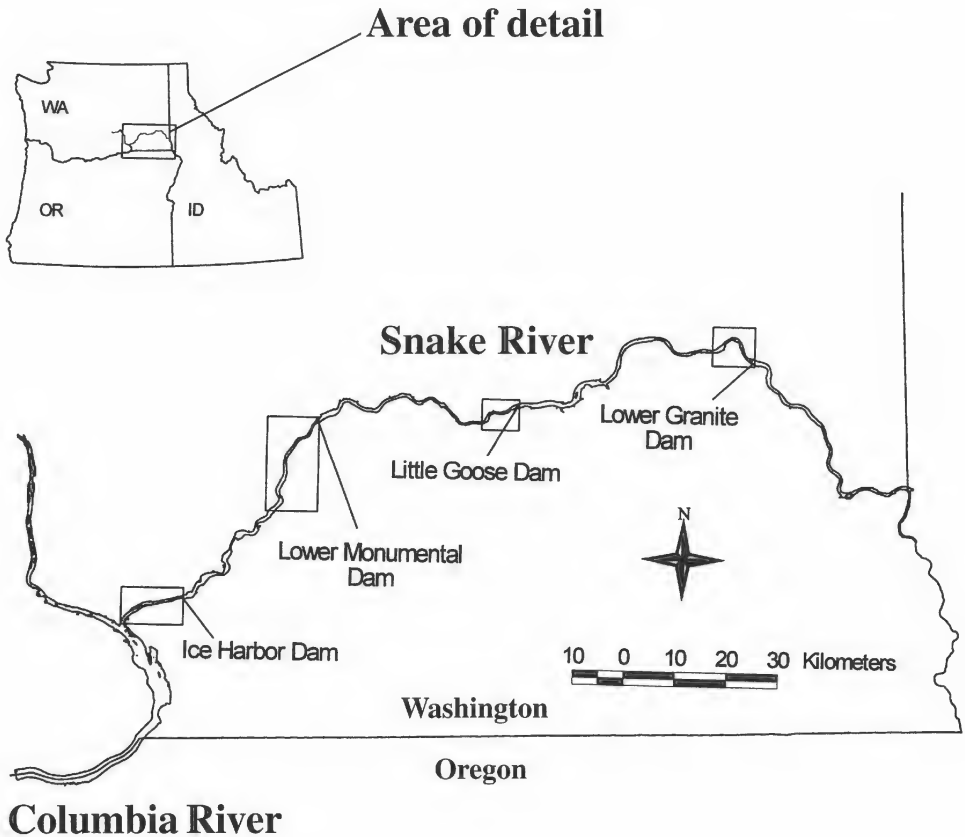

Figure 1. Areas along the lower Snake River where sampling for white sturgeon eggs was performed during 1993-95 and 1997-98.

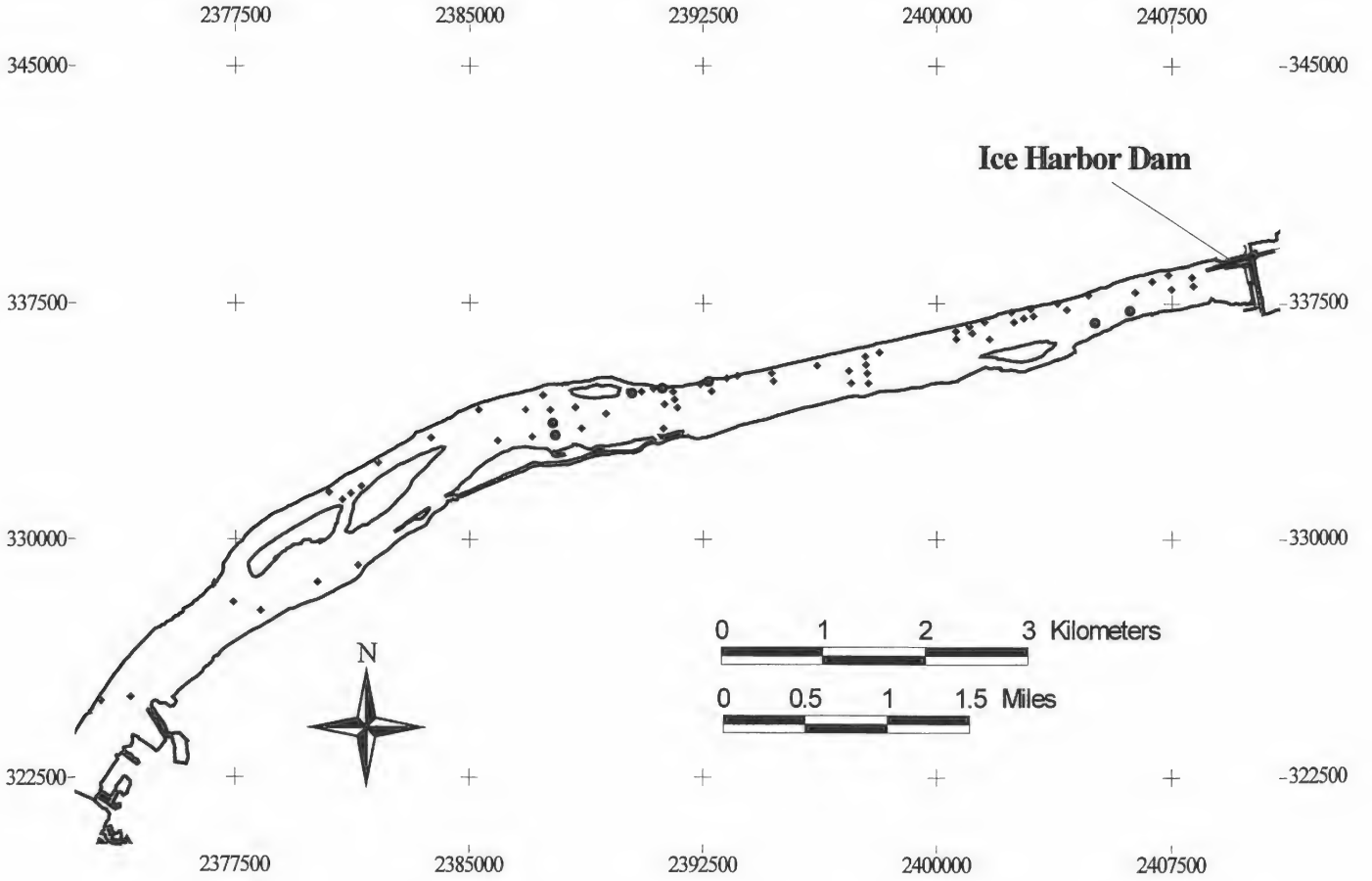

Figure 2. Sites sampled with artificial substrates or plankton nets in McNary Reservoir downstream from Ice Harbor Dam during 1993-95. Black circles depict sites where eggs were collected, and black diamonds depict sites where no eggs were collected. Graticules are in the State Plane Coordinate System, Washington South Zone. The horizontal datum used was NAD27.

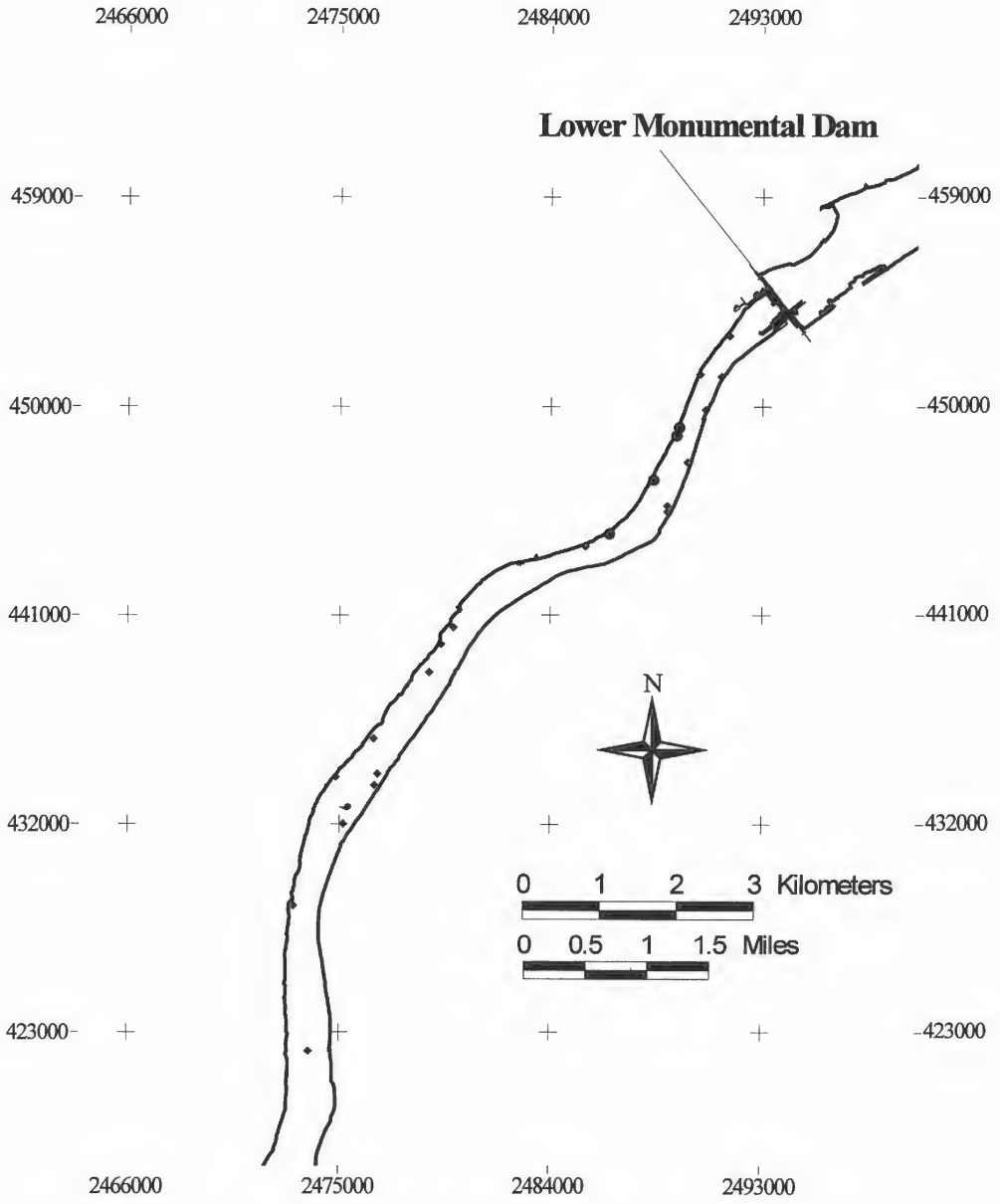

Figure 3. Sites sampled with artificial substrates in Ice Harbor Reservoir downstream from Lower Monumental Dam during 1997-98. Black circles depict sites where eggs were collected, and black diamonds depict sites where no eggs were collected. Graticules are in the State Plane Coordinate System, Washington South Zone. The horizontal datum used was NAD27.

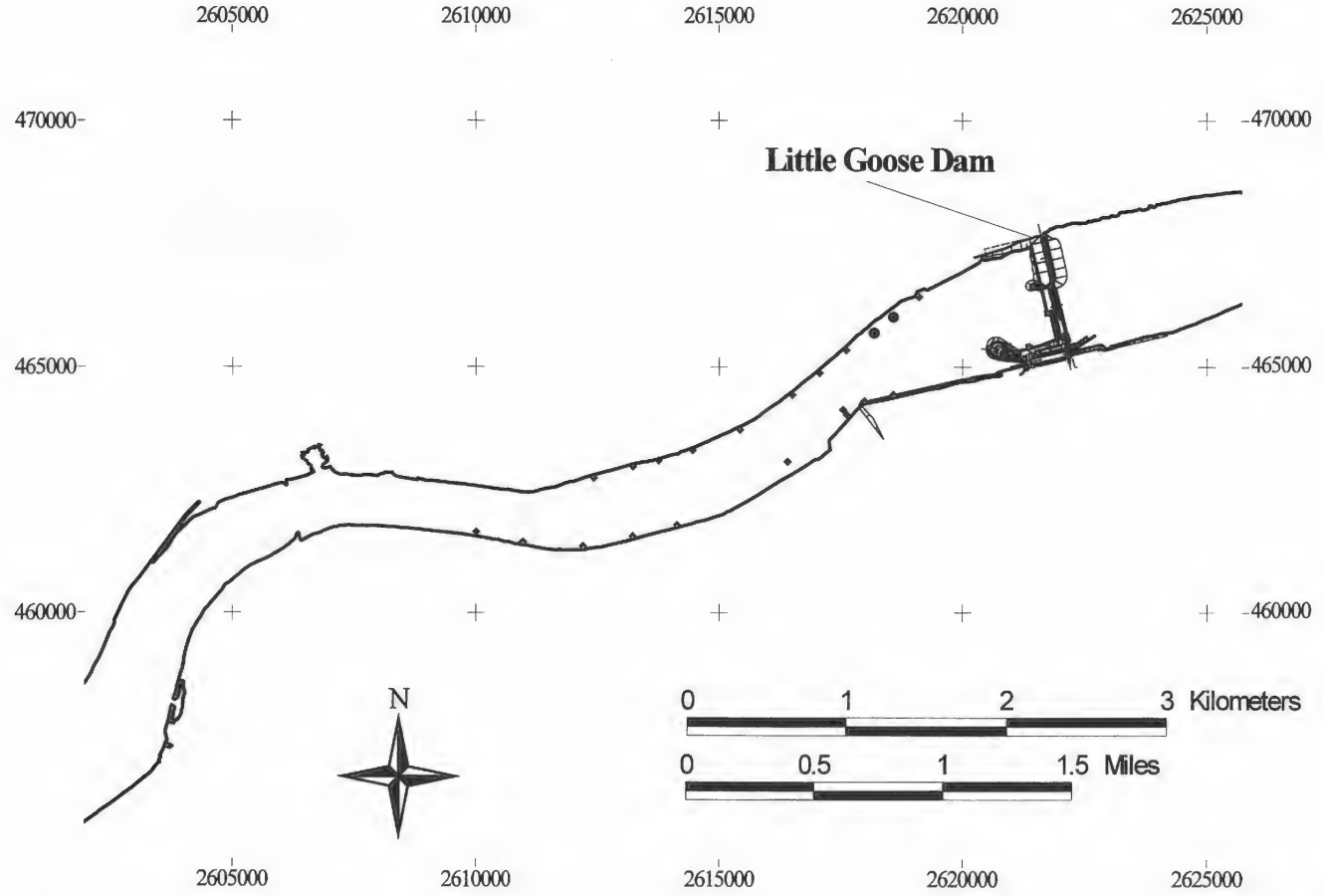

Figure 4. Sites sampled with artificial substrates in Lower Monumental Reservoir downstream from Little Goose Dam during 1997-98. Black circles depict sites where eggs were collected, and black diamonds depict sites where no eggs were collected. Graticules are in the State Plane Coordinate System, Washington South Zone. The horizontal datum used was NAD27.

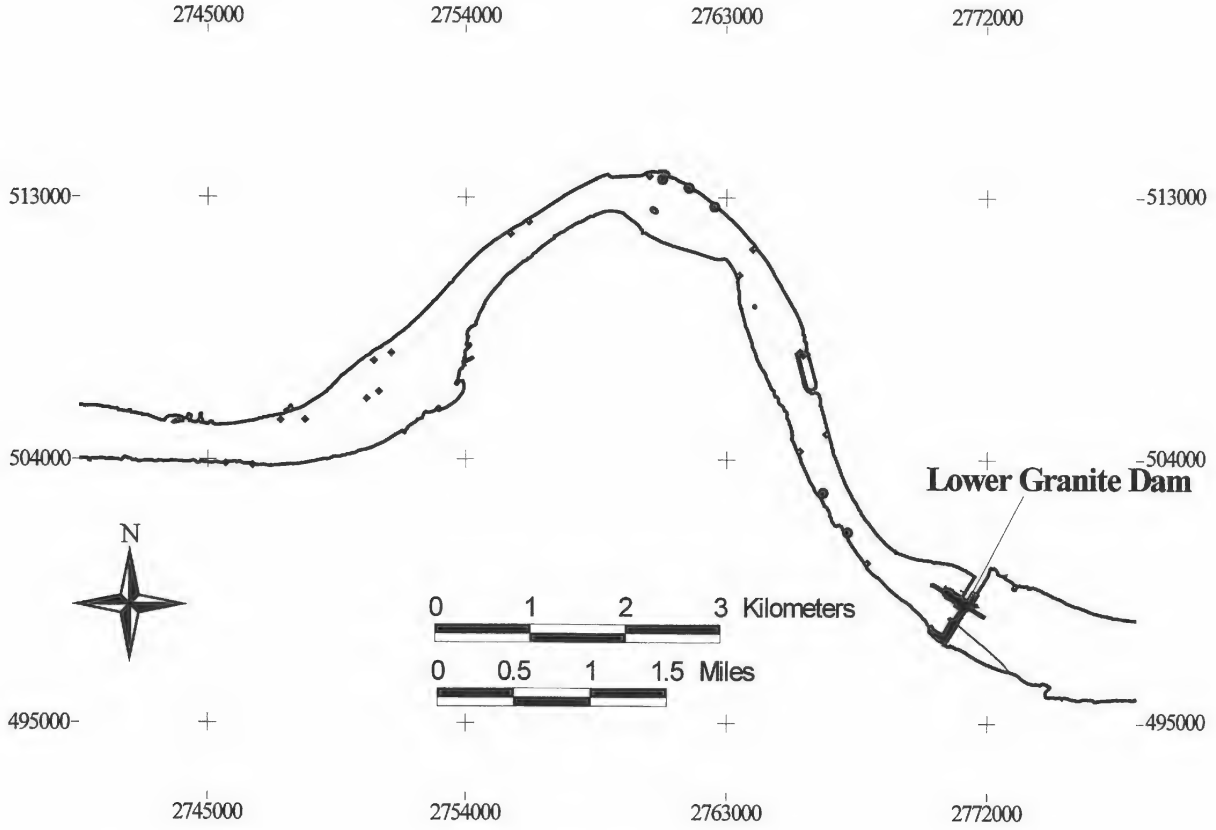

Figure 5. Sites sampled with artificial substrates in Little Goose Reservoir downstream from Lower Granite Dam during 1997-98. Black circles depict sites where eggs were collected, and black diamonds depict sites where no eggs were collected. Graticules are in the State Plane Coordinate System, Washington South Zone. The horizontal datum used was NAD27.

peratures exceeded 19°C. This corresponded to a period from mid-May to mid-July during all years.

The sampling gears used to collect eggs included U-shaped plankton nets (Parsley et al. 1993) and artificial substrates (McCabe and Beckman 1990). The U-shaped plankton nets were used only downstream from Ice Harbor Dam. They were constructed of 1.59-mm knotless mesh attached to an inverted U-shaped frame. Two spherical lead weights (4.5 kg each) were attached to the lower corners of the frame. Paired plankton nets were fished by anchoring the vessel at the sampling site and lowering the nets until they made contact with the bottom of the river. Generally, the nets were fished at each site for 30 min once or twice weekly. We modified the design of the artificial substrates used by McCabe and Beckman (1990) by adding an additional cross-brace to each side of the frame to better support the filter material. Artificial substrates were deployed at sampling sites and typically checked once weekly. White sturgeon eggs were readily identified in the field from other eggs collected by their large size and opaque coloration. Weekly retrieval of the artificial substrates and deployment of the U-shaped plankton nets was occasionally interrupted by mechanical problems, severe weather, or high river discharges that created dangerous sampling conditions.

While sampling downstream from Ice Harbor Dam, we mapped and navigated to sampling sites using river navigation charts and visual markers. Sampling sites that were plotted on the navigation charts were transferred into a geographic information system (GIS) by assigning geographic coordinates using the State Plane Coordinate System, North American Datum of 1927 (NAD27), Washington South Zone. These coordinates were used within the GIS to generate the map of sampling sites in the Snake River section of McNary Reservoir (Figure 2).

Sampling sites in Ice Harbor, Lower Monumental, and Little Goose reservoirs were recorded with a Rockwell[2] PLGR+ Global Positioning System (GPS) receiver using Precise Positioning Service[3]. The NAD27 was used as the datum for all recorded GPS positions. Position coordinates were converted to the State Plane Coordinate System, Washington South Zone, then directly downloaded into a GIS to generate the maps of sampling sites for Ice Harbor, Lower Monumental, and Little Goose reservoirs (Figures 3, 4, and 5).

Results

We sampled for white sturgeon eggs at a number of sites in the lower Snake River, and identified 17 sites where spawning occurred. Sampling effort was not equal among reservoirs and years, and two gears were used in Ice Harbor Reservoir. White sturgeon spawning was documented in McNary, Ice Harbor, Lower Monumental, and Little Goose reservoirs (Table1), and all white sturgeon eggs were collected between 1.0 and 7.0 km downstream from a dam. White sturgeon are broadcast spawners, and our sampling methods allowed us to collect eggs where they settled on the substrate. Thus, exact locations where spawning occurred were not determined, but spawning and egg incubation sites must be in close proximity to each other.

Spawning by white sturgeon in the Snake River downstream from Ice Harbor Dam occurred further downstream from this dam (7.0 km) than spawning occurred downstream from the other three dams. Sampling in McNary Reservoir was performed during 1993 through 1995 between river km 3.2 to 15.1, and all white sturgeon eggs were collected between 1.2 and 7.0 km downstream from Ice Harbor Dam (Figure 2). Spawning by white sturgeon in this river reach occurred in several areas, based on our collection of 245 eggs from seven sites (Table 1). At these seven sites, eggs were collected with artificial substrates from the lower two sites and the upper two sites, and eggs were collected in the plankton nets at the other three sites as well as at the lower two sites.

Spawning by white sturgeon in Ice Harbor Reservoir occurred within 3.9 km downstream from Lower Monumental Dam (Figure 3). Sampling in Ice Harbor Reservoir was performed between river km 56.0 to 65.5, and all white sturgeon eggs were collected between 2.0 and 4.0 km downstream from Lower Monumental Dam. We collected 22 eggs at three sites in Ice Harbor Reservoir during 1997 and 1998 (Table 1). The spawning occurred within a 1.8-km reach along the north shoreline.

Spawning by white sturgeon in Lower Monumental Reservoir occurred within 1.0 km of Little Goose Dam. Sampling during 1997 and 1998 was

TABLE 1. Characteristics of locations where white sturgeon eggs were collected in the lower Snake River. State Plane coordinates can be used to locate the sites on the accompanying figures, or used as input into a geographic information system. The coordinates use the horizontal datum NAD27 and are in Washington South Zone.

Reservoir	Depth[1] (m)	Geographic coordinates		Number of eggs collected[2]	
		Northing	Easting	1993-95	1997-98
McNary	5	333716	2387658	179	—
McNary	5	333286	2387769	39	—
McNary	7	334636	2390205	3	—
McNary	8	334790	2391183	1	—
McNary	8	335009	2392662	1	—
McNary	3	336882	2405061	21	—
McNary	5	337264	2406167	1	—
Ice Harbor	6	444505	2486517	—	7
Ice Harbor	7	446831	2488390	—	2
Ice Harbor	6	449119	2489475	—	13
Lower Monumental	7	465331	2617624	—	16
Lower Monumental	8	466005	2618588	—	14
Little Goose	5	513615	2760782	—	1
Little Goose	8	513328	2761701	—	2
Little Goose	8	512681	2762584	—	272
Little Goose	8	502856	2766321	—	2
Little Goose	8	501508	2767172	—	187

[1]Depths are approximate due to varying pool elevations.
[2]Dashes indicate years when no sampling was performed in the reservoir.

performed between river km 109.6 and 112.5. During our sampling, we collected 30 eggs from two sites in Lower Monumental Reservoir (Table 1). Both sites were located along the north shoreline within 200 m of each other. Eggs were not collected with artificial substrates located immediately upstream or downstream from these sites, suggesting that this spawning area is rather limited in extent. All white sturgeon eggs collected in Lower Monumental reservoir were collected between 1.0 and 1.2 km downstream from Little Goose Dam (Figure 4).

We collected 464 eggs at five sites in Little Goose Reservoir during 1997 and 1998 (Table 1). Sampling was performed between river km 161.0 to 171.9. All white sturgeon eggs collected in Little Goose Reservoir were collected between 1.3 and 5.8 km downstream from Lower Granite Dam (Figure 5). Spawning occurred in two general areas, both on outside bends of the river channel. Two of the artificial substrates fished in these areas (one from each general area) collected the majority of the eggs. One artificial substrate in the lower of the two areas collected 272 eggs, and an artificial substrate in the upper area collected 187 eggs for a total of 459 eggs. The remaining five eggs were collected at three sites near the two artificial substrates where most of the eggs were collected. Eggs were not collected on artificial substrates located just upstream and downstream from these areas (Figure 5). Thus, we believe that these spawning areas are limited in extent.

Discussion

Although fisheries for white sturgeon in the Columbia River Basin have been regulated for over 100 years, it wasn't until 1983 that spawning areas used by these fish were documented. During that year, employees from the Washington Department of Fisheries collected fertilized eggs downstream from Bonneville Dam (J.D. DeVore, Washington Department of Fish and Wildlife, pers. comm.). Spawning has since been documented in several reservoirs and river reaches in the Columbia River Basin. Spawning has been documented in the Columbia River downstream from Bonneville, The Dalles, John Day, and McNary dams (Parsley et al. 1993, McCabe and Tracy 1994), downstream from Priest Rapids dam (authors, unpublished data), and at the confluence of the Pend d'Orelle River (R.L. & L. Environmental Services Ltd. 1994). Spawning by white sturgeon has also been documented in the middle

Snake River (K. Lepla, Idaho Power Company, pers. comm.) and Kootenai River (V. Paragamian, Idaho Fish and Game, pers. comm.).

The documentation of spawning areas is important because this habitat is necessary to maintain natural and viable populations. The information presented here identifies, within meters, areas where white sturgeon have spawned. We believe that spawning by white sturgeon in the lower Snake River may occur in other locations near the sites we sampled because hydrologic and thus habitat conditions vary from year to year. However, it is unlikely that spawning occurs much further downstream from where we collected eggs because the water velocities, an important physical microhabitat variable for spawning (Parsley and Beckman 1994) decrease rapidly due to the backwater effects caused by the downstream dam. Although no historic record of spawning sites exists for the lower Snake River, it is probable that prior to impoundment, spawning occurred in favorable locations throughout the lower Snake River.

The identification of white sturgeon spawning areas is aided by the descriptions of spawning habitat provided by Parsley et al. (1993) and McCabe and Tracy (1994), who described the physical characteristics of white sturgeon spawning habitat in the Columbia River in detail. Although we did not measure water velocities in this study, the sites where we collected eggs had very high, turbulent velocities. Sites where eggs were not collected generally had lower or more laminar velocities. The sites where eggs were collected were often near river bends or areas with variable bottom topography that created constantly changing eddies and currents. Habitats such as this may allow white sturgeon to hold position in these high velocity environments while at the same time providing good dispersal of the adhesive eggs.

The artificial substrates we used enable sampling in a variety of habitats, but there were areas downstream from the dams that possess characteristic white sturgeon spawning habitat that we could not or would not sample. Those areas include the federally maintained navigation channel and the boat restricted zone downstream from each dam. Generally, sampling was precluded from these areas by excessive water velocities, large standing waves, or other conditions that made these areas unsafe for the sampling crews.

The amount of available spawning habitat for white sturgeon increases and decreases on an arrhythmic and seasonal basis because of differences in river discharge and water temperature (Parsley and Beckman 1994). These in turn are influenced by natural fluctuations in hydrologic conditions and the need to meet power production, flood control, and irrigation requirements. Currently, there are proposals to alter the management of the water storage projects on the Columbia and Snake rivers to increase survival of juvenile anadromous salmonids. If management of the hydropower system changes to restore a more natural river, we could see an increase in available spawning habitat and activity that would be beneficial to sustaining these white sturgeon populations (Auer 1996, Beamesderfer et al. 1995).

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Footnotes

1. The mention of trade names does not imply endorsement by the U.S. Geological Survey.
2. The Precise Positioning Service (PPS) is available to the military and certain federal civilian agencies. This Global Positioning System service differs from the Standard Positioning Service available to civilian users; PPS provides an accurate position (currently ±10-m without performing differential corrections.

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Taxonomy and Distribution of the Malheur Mottled Sculpin, *Cottus bendirei*

Abstract

The taxonomy of mottled sculpins (*Cottus bairdi* complex) in Harney Basin, Oregon was reviewed and diagnostic characters were evaluated. The literature and current data support recognition of two species, Malheur mottled sculpin (*C. bendirei*) and Columbia mottled sculpin (*C. hubbsi*). Counts of body prickles on the left side, completeness of lateral line and relative head size were used to classify Harney Basin individuals. Both species occurred in northern Harney Basin and hybrids were found at contact zones in Silver and Silvies rivers. *Cottus hubbsi* appeared dominant in mainstem Silvies R. with *C. bendirei* upstream and in isolated creeks. *Cottus bendirei* was the only species in southern Harney Basin. Both species also occurred outside Harney Basin in the Malheur and Snake rivers, lower Columbia Basin, and probably the upper Columbia Basin. An alternative hypothesis, that these forms represent a single polymorphic species or ecotype, was tentatively rejected because the congruence of morphology and distribution was consistent with two species meeting in a narrow hybrid zone. A better understanding of reproduction, development and the dynamics of sculpin hybrid contact zones is needed to resolve the question.

Introduction

The mottled sculpin complex, *Cottus bairdi* (Girard, 1850), is widespread in eastern and western North America but with a significant distributional gap in central North America. Jenkins and Burkhead (1993) and others have noted that the four recognized subspecies are poorly understood and redefinition of this complex is needed. In western North America two subspecies are recognized by Bond (1963): *C. b. punctulatus* (Gill, 1861) a smooth skin form in the Upper Colorado River and *C. b. semiscaber* (Cope, 1872) of the Columbia R. *Cottus semiscaber* was described from the Upper Snake R. above American Falls (Fort Hall, ID) as prickled above the lateral line and with a lateral line "discontinued on the last fourth of caudal peduncle." Within the Columbia Basin, there are two additional named, but unrecognized, taxa—*C. hubbsi* Bailey and Dimick, 1949 and *C. bendirei* (Bean, 1881).

Cottus hubbsi was described from the upper Columbia River in Washington and Salmon River of Idaho (a lower Snake R. tributary). It is prickled, with a complete or almost complete lateral line and is generally treated as a synonym of *C. b. semiscaber.* However, Peden et al. (1989) suggest resurrecting *C. hubbsi* for "*C. bairdi* of western North American." As demonstrated by Peden et al. (1989), taxonomic problems of the *C. bairdi* complex include other species which are similar or with which they may hybridize—*C. rhotheus* (Smith, 1882), *C. cognatus* Richardson, 1836, and *C. confusus* Bailey and Bond, 1963.

The Malheur mottled sculpin, *C. bendirei*, was originally collected in Rattlesnake Cr., a small, disconnected stream in Harney Co., Oregon. In the original description, Bean (1881) noted lack of body prickles, four preopercle spines with longest about one half of eye diameter, and three pelvic fin rays. Snyder (1908), examining 30 specimens from Silver Cr., also noted the "entirely smooth" body, but found three or four preopercular spines with the fourth always minute and three or four pelvic rays with the fourth often small. He also reported correspondence with Bean who re-examined the holotype and found a rudimentary fourth pelvic ray on the right side and three on the left. In contrast, Schultz (1936) described *C. bendirei* as having head and body usually with prickles, longest preopercular spine one half to two thirds eye diameter, and three or four pelvic rays. Bond (1963) attributes the discrepancy in body prickles to another form of mottled sculpin from Silvies R. and Donner und Blitzen drainage. The three-or-four pelvic fin ray issue was again discussed by Bailey and Dimick (1949), who also noted the holotype had three on the left and four on the right (based on R. Miller's observations), and by Bond (1963) who noted that *C. bendirei* has a reduced fourth pelvic ray. Bond (1963) also contrasted smooth skin and a longer (complete) lateral line in nominal *C. bendirei* than in Silvies/ Blitzen mottled sculpin which he found

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are more typical of *C. b. semiscaber*. He also was the first to report the smooth skin form in disconnected streams in other parts of the basin, Riddle Cr. and Silver Cr. In contrast, Bison and Bond (1971) characterize *C. bendirei* from isolated creeks as having a short lateral line. They also re-classify fish from the Malheur Basin. Donner und Blitzen R. fish plus those from the isolated creeks and Scotty Cr. in the upper Silvies R. have a "pronounced resemblance" to *C. b. semiscaber* as well as "some likeness" to *C. b. punctulatus* (presumably that they are mostly naked). In contrast, heavily-prickled, complete lateral line sculpins of Silvies R. mainstem are "markedly different" and have a greater affinity for nominal *C. hubbsi* of the central and lower Columbia R. Subsequently and without comment on Silvies R. fish, Bond (1983) notes that fish from Donner und Blitzen R. might have light prickles and "not be typical" of *C. bendirei* found in Poison, Devine Canyon, Smyth, Riddell and Silver creeks.

Further complicating the taxonomy of sculpins is evidence of diagnostic characters being influenced by environment or ontogeny. Reduced body prickling has been associated with headwater streams and riffle habitat in some *Cottus* species (Jenkins and Burkhead, 1993) or small size in *C. asper* (Krejsa, 1965). Completeness of lateral line pores has been positively correlated to size in sculpins, hence adults may have a more complete lateral line (Koli 1969; Janssen et al. 1987).

Although the iterations in understanding are confusing, the current wisdom is that Malheur mottled sculpin is a smooth-skinned (non-prickled), reduced lateral line form of the predominantly prickled subspecies, *C. b. semiscaber,* now thought to be broadly distributed in the western U. S. with both smooth and prickled forms. Although its identity and distribution are unclear, the State of Oregon considers the Malheur mottled sculpin (smooth skin *C. bendirei*) as a "sensitive-critical" species because the population in Rattlesnake Cr. is extinct and others are presumed hybridizing with *C. hubbsi* (Bisson and Bond 1971). Because the Malheur mottled sculpin has been labelled "distinct" and "vulnerable to extinction," the purpose of this study was to evaluate diagnostic characters to determine if evidence supports recognition as a distinct taxon, and if so, its current distribution.

Description of Area

Harney Basin, a 5,300 sq. mi. closed depression in Oregon's High Lava Plains physiographic province (Figure 1) is bordered by Miocene basalts and evolved as a downwarp assisted by collapsing calderas about 7-9 million years before present (mybp) (Orr, et al. 1992). Its northwestern margin is the Blue Mountains province, a region of uplift and vulcanism at least 65 mybp. The stage of valley development along the northwestern margin suggested to Bisson and Bond (1971) that "ample opportunity has existed for stream capture between the John Day (a Columbia R. tributary) and Silvies drainages". The eastern and southern margins are the basin and range province with Steens Mt. in the southeast and the northwest-tending Brothers fault zone along its western margin (Orr, et al. 1992). During the Pleistocene, Silvies R. is thought to have drained east through Malheur R. to the Snake R. until lava flows dammed the outlet creating Lake Malheur (Hubbs and Miller 1948). Today, the basin has isolated, disconnected creeks plus two shallow ephermeral lakes, Malheur and Harney lakes and their tributaries (Figure 1). A third, smaller lake, Mud Lake, sometimes connects the other two.

Materials and Methods

Museum acronyms are USNM – U. S. National Museum and OS – Oregon State University Fish Collection. Specimens from Harney Basin were grouped into two subbasins: 1) northern - Silver R. and its tributaries; Silvies R. and its tributaries; and isolated northern creeks, including Rattlesnake and Devine Canyon creeks; and 2) southern - Donner und Blitzen R., its tributaries and isolated southern creeks, including Riddle Cr. (Figure 1). Comparisons are made with other *C. bairdi* complex from the Snake R. basin and the Columbia Basin below the confluence with the Snake R and with *C. confusus* and *C. rhotheus* (Table 1).

Characters selected for study were those identified in the literature. The following measurements were taken with digital calipers - standard length (SL); head length (HL); caudal peduncle depth (CPD); and length of third and fourth pelvic fin rays. Corrections for allometric changes in HL and CPD were made by using residuals from linear regression of the body part on SL. Percent completion of the lateral line was estimated by dividing the distance from the first pore to the last pore by the distance from the first pore to the base of the hypural plates (posterior point of SL

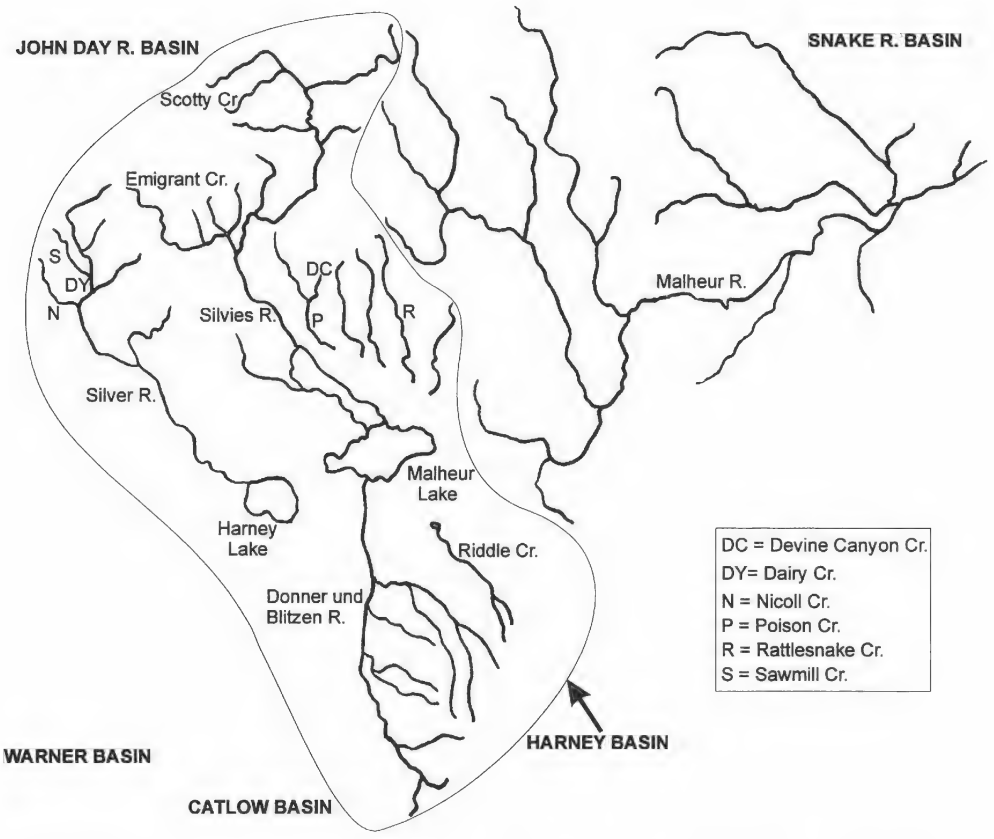

Figure 1. Map of Harney Basin showing major drainages and relationship of the basin to Malheur R. and adjacent basins.

measurement). The last canal pore did not include single disjunct segments on the caudal peduncle but did include multiple disjunct segments. We counted pectoral fin rays; pelvic fin rays; and total number of prickles on the left lateral body surface. Prickles were counted on paper towel- and air-dried specimens under a dissecting microscope and all prickle counts greater than 99 were scored as 100.

Our procedure was to initially restrict the analysis to northern Harney Basin samples. We used number of prickles on the left side (the most obvious bimodally distributed character and the character most often discussed in the literature) to assign specimens to species and evaluated whether other characters corroborated the classification. Statistical analyses were performed using Statgraphics (Statistical Graphics Corporation, vers. 2.1).

Distributional information is based on literature, museum collections and recent surveys made in northern Harney Basin in 1994 and 1997 and in headwater streams of the John Day R. and western portions of the Malheur R. in 1997. Voucher specimens retained for OS were either fixed in 10% formalin with subsequent preservation in 50% isopropanol, or preserved in 95% ethanol.

Results

Northern Harney Basin

The distribution of prickles on the left side shows three distinct groups with *C. bendirei* having a mean of 2.2 (range: 0-19), *C. hubbsi* a mean of

TABLE 1. List of specimens examined for morphology and distributional information. The number following the catalog number is the number of specimens in the lot. Ethanol preserved samples indicated with asterisk.

Species	Basin	Water body
C. bairdi	Mississippi	Ohio, Mahoning R. USNM 24843 (holotype), 1
C. bendirei	Northern Harney	Sawmill Cr. ,OS 14890*, 33; OS 14893, 19; OS 14896*, 15; OS 14897, 13; Dairy Cr. OS 14894*, 13; Silver Cr. OS 14898*, 10; OS 14899, 9, OS 15069, 8; OS 15070, 7, OS 15071, 3; Nicoll Cr. OS 14900*; OS 14901* 11; OS 14902, 6; Silver R. OS 16674, 18; Dodson Cr. OS 15068, 10; Wickiup Cr. OS 15072, 5; Scotty Cr. OS 2538, 4; OS 10827, 1; OS 10851, 2; OS 15182*, 5; OS 16703, 15; Emigrant Cr OS 16707, 17; Myrtle Cr. OS 15185*, 3; Camp Cr. OS 15186*, 3; Bear Cr. OS 2540, 2; Rattlesnake Cr. USNM 24196 (holotype of P. bendirei), 1; OS 351, 1; OS 533, 4; Devine Canyon Cr. OS 14889*, 12; Poison Cr. OS 16685, 1; OS 16706, 19.
C. hubbsi	Northern Harney	Silvies R. OS 15183*, 2; OS 15187*, 2; OS 16695, 17; OS 2559, 1; OS 457, 8; OS 2543, 38; OS 2544, 4; OS 2539, 11; OS 2550, 23;
C. bendirei	Southern Harney	Donner und Blitzen R. OS 10383, 3; OS 2547,4 ; OS 325, 3; OS 2548, 18; Mud Cr. OS 538, 9; Big Indian Cr. OS 7432, 5; Kiger Cr. OS 503, 9; Riddle Cr. OS 2541, 55
C. bendirei	Columbia-Snake R.	Malheur R. OS 16708, 18; OS 16687, 1.; OS 16697, 5
C. hubbsi	Columbia-Snake R.	Malheur R. OS 16708, 18; OS 752, 14; Wallowa R OS 619, 1; OS 5813, 4; Imnaha R. OS 5419, 10; St. Charles Cr. OS 5590, 13; Snake R. OS 8366, 4; Boise R.; OS 15529, 5; OS 15531, 5; Powder R. OS 9297, 3
C. bendirei	lower Columbia	Clatskanie R. OS 9809, 2; Willamette R. OS 6810, 4; OS 10028, 1; OS 11021, 1; OS 10208, 1; OS 9403, 1; OS 15731, 2; OS 17088, 5; OS 627, 48; Gales Cr.; OS 14426, 2; OS 14408, 9; OS uncataloged, 16
C. confusus.	lower Columbia	Willamette R. OS 544, 3; Santiam R. OS 9978, 5; Columbia R. OS 15608, 2; OS 15600, 4; OS 15601, 4
C. rhotheus	Columbia	John Day R. OS 2552, 4; OS 2556, 3; Willamette R. OS 648, 1; OS 9498, 1; OS 15705, 2; OS 960, 1; Bear Cr. OS 16456, 2; Columbia R. OS 953, 3,
	Coastal	Necanicum R. OS 10934, 5

100+ (range >99), and nominal hybrids a mean of 53.8 (range 33-70) (Figure 2a). There was no difference in SL (P=0.71) between *C. bendirei* ($\bar{x}$=47.7 mm), *C. hubbsi* ($\bar{x}$=46.3 mm) and hybrids ($\bar{x}$=44.5 mm). Mean percent completion of the lateral line (Figure 3a) was lowest in *C. bendirei* (89.5%), highest in *C. hubbsi* (98.3%) and intermediate in hybrids (93.2%). Hybrids had the highest variance (Figure 3a). Differences in lateral line completeness between species were significant (P<0.0001) as were differences between hybrids and *C. hubbsi* (P=0.008). Differences between *C. bendirei* and hybrids were not significant (P=0.16). Head lengths were related to SL by the relationship HL= 0.2238 + 0.3115SL (r^2=96.3%, P<0.001). Residuals from this relationship showed that for a given size, *C. bendirei* had a significantly (P<0.001) smaller head than *C. hubbsi* or hybrids (Figures 3b and 4). Hybrids and *C. hubbsi* were not significantly different in HL residuals (P=0.9231). Caudal peduncle depth (CPD) was related to SL by the relationship CPD=0.2162+ 0.0759 SL (r^2=96.2, P<0.001). Residuals from this relationship were not significantly different between species or hybrids (P=0.62). The length of the fourth pelvic ray, expressed as a percent of the length of the third pelvic ray, was not significantly different (P=0.23) though it tended to be smaller in hybrids and *C. bendirei* (Figure 3c). Number of pectoral fin rays (range 14-16) and number of pelvic fin rays (range 3-4) were not significantly different between species and their hybrids (P>0.12).

Cottus bendirei was the dominant or only species in isolated streams and upstream tributaries and *C. hubbsi* was the dominant or only species in the mainstem Silvies R. (Figure 5a). Hybrids were geographically restricted to contact zones

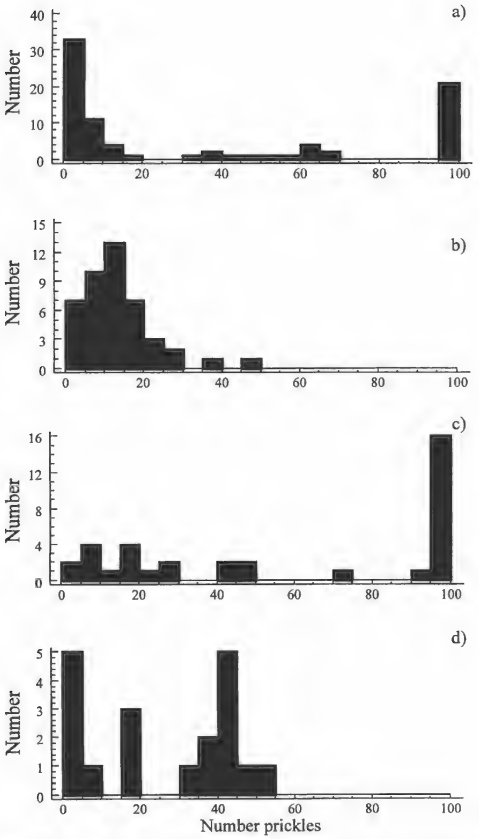

Figure 2. Frequency distribution of number of body prickles on the left side: a) northern Harney Basin; b) southern Harney Basin; c) Snake R. basin, including Malheur R.; d) lower Columbia Basin.

between the two species and were found twice with *C. bendirei* (OS 14897, OS 16707), once with *C. hubbsi* (OS 2544), and once alone (OS 15185 with three specimens).

Southern Harney Basin

There was no evidence of *C. hubbsi* in southern Harney Basin, but counts of body prickles suggested presence of two hybrids (Figure 2b). There was no difference in SL (P=0.94) between *C. bendirei* ($\bar{x}$=51.3 mm) and those two fish ($\bar{x}$=52.1 mm). Mean prickle counts of *C. bendirei* in southern Harney Basin were higher (10.1) than in northern fish, but much lower than *C. hubbsi* (Figure 2). Mean percent completion of the lateral line

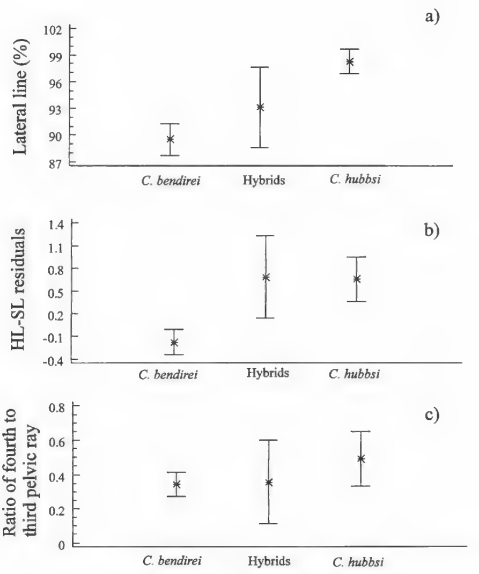

Figure 3. Frequency distribution of selected characters of northern Harney Basin mottled sculpins; a) percent completion of lateral line; b) relative head length, expressed as a residual from the relationship, HL= 0.2238 + 0.3115SL; c) relative length of the fourth pelvic fin ray, expressed as a percent of the length of the third pelvic fin ray.

(87.2%) was even lower than in northern *C. bendirei*. Head size, as a residual from the relationship, HL= 0.2238 + 0.3115SL, was negative ($\bar{x}$= –0.74), indicating that southern Harney Basin *C. bendirei* have even shorter heads than those from the northern basin.

Snake River Basin

Samples from Snake R. Basin, including Malheur R., contained both species plus hybrids. There was no difference in SL (P=0.24) between *C. bendirei* ($\bar{x}$=43.6 mm) and *C. hubbsi* ($\bar{x}$=50.4 mm), but hybrids were significantly (P=0.04) smaller ($\bar{x}$=29.5 mm). Mean prickle counts in the Snake River Basin were 11.8 for *C. bendirei*, similar to counts for southern Harney Basin (Figures 2b and 2c). Head size, as a residual from the relationship, HL= 0.2238 + 0.3115SL, was not significantly different between species (P=0.10), though the mean was smaller for *C. bendirei* (0.25) than *C. hubbsi* (0.61). Mean percent completion of the

Figure 4. Mottled sculpins from eastern Oregon: a) *C. bendirei,* OS 16706, 81.9 mm SL, Poison Cr.; b) hybrid - *C. bendirei* X *C. hubbsi*, OS 14897, 75.5 mm SL, Sawmill Cr.; c) *C. hubbsi*, OS 619, 70.5 mm SL, Wallowa R.

lateral line was low in *C. bendirei* (93.8%) and high in *C. hubbsi* (98.4%) but differences were again not significant (P=0.13). One sample from Drewsey Grange, Malheur R. (OS 16708) contained both species plus hybrids.

Lower Columbia Basin

There was no evidence of *C. hubbsi* in the Willamette R. or lower Columbia Basin, but counts of body prickles suggested a high proportion of hybrids (Figure 2d). There was no difference in SL (P=0.67) between *C. bendirei* ($\bar{x}$=65.8 mm) and hybrids ($\bar{x}$=63.1 mm). Mean prickle counts in the lower Columbia Basin were 6.4 for *C. bendirei* and 42.6 for hybrids. Head size, as a residual from the relationship, HL=0.2238 + 0.3115SL, was not significantly different between *C. bendirei* and hybrids (P=0.52), but the mean was smaller for *C. bendirei* (-0.56) than for hybrids (-0.21). Mean percent completion of the lateral line was high in *C. bendirei* (97.2%) and even higher in hybrids (98.2%) but differences were again not significant (P=0.45).

Distribution of the Western *C. bairdi* Complex

Members of the *C. bairdi* complex are widely distributed in western North America (Figure 5b). In the upper Columbia they are known from Yakima, Okanongan, Similkameen and Methow

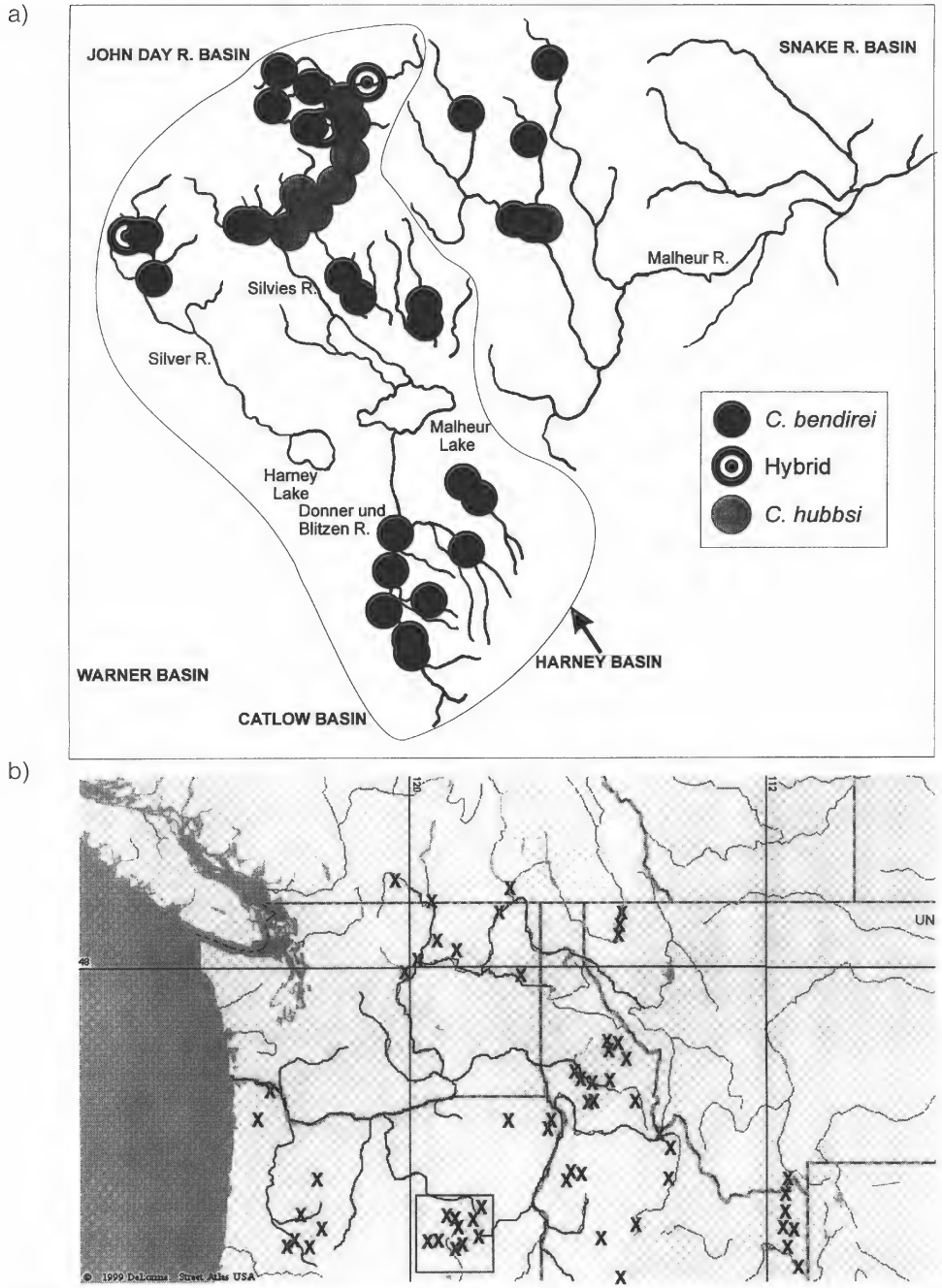

Figure 5. a) Map of Harney Basin showing distribution of *C. bendirei, C. hubbsi* and their hybrids. b) Map of Columbia Basin showing distribution of *C. bairdi* complex. Upper Columbia records from Peden et al. (1989); Idaho records from Simpson and Wallace (1978); Oregon records from this study. Box outlines area of map above.

rivers (Peden et al 1989; M. Hallock, Washington Dept. Fish and Wildlife, pers. comm, 1999). However, they are noticeably absent from the mainstem of lower and middle Columbia R., the mainstem of the Willamette R., all of the Deschutes R., all of the John Day R., and the lower Snake R. Bisson and Bond's (1971) table showing it in the John Day R. may be erroneous. During recent directed surveys in and around Harney Basin, no mottled sculpin were found in the John Day drainage and recent field biologists are unaware of its presence in John Day drainage (H. Li, pers. comm., June, 1999, Oregon Cooperative Fisheries Research Unit). A single specimen (OS 5512) is known from the John Day drainage but it can not be the basis for Bisson and Bond's (1971) record because it was collected five years later (1976) by an ichthyology class. The location is presumed in error pending additional verifiable collections. Also a Puget Sound record (Wydoski and Whitney 1979) is now believed to be a mis-identifcation (M. Hallock, Washington Dept. Fish and Wildlife, pers. comm, 1999).

Disjunct distributions were also evident at smaller spatial scales. In the Willamette and lower Columbia, most *C. bendirei* were downstream near the mouth of the Willamette and Clatskanie rivers while hybrids were upstream (Figure 5b).

Discussion

The literature and current data support our hypothesis of two species of mottled sculpins, *C. bendirei* and *C. hubbsi,* in Oregon. Fish from northern Harney Basin most clearly supported our hypothesis, in part, we believe, because of large sample sizes and broad distribution of sample sites (Table 1; Figure 5a). Both species segregated geographically (Figure 5a) and had geographically restricted contact zones in which hybrids were found. *Cottus hubbsi* appeared restricted to river mainstems (primarily Silvies R.) while *C. bendirei* was in smaller tributaries and disconnected streams.

Hybrids are often, though not always, intermediate in characters between parent species (Neff and Smith 1979; Leary *et al* 1985). Our preliminary identification of northern Harney Basin hybrids is based on intermediacy of prickles (Figure 2a) and lateral line completion (Figure 3a) plus the inconsistent patterns found in other characters. For example, hybrids were more like *C. hubbsi* in head length (Figure 3b) but more like *C. bendirei* in reduction of the fourth pelvic fin ray (Figure 3c). In addition, most hybrids were found in areas where both species come in contact (Figure 5a) and four of five samples with hybrids also contained one or both parent species.

Southern Harney Basin also was well sampled and sample sizes were large (Table 1; Figure 2), but we believe only one species, *C. bendirei*, was present. Two specimens with more than 35 prickles must be considered questionable. Diagnostic characters useful in the northern part of the basin also applied here. In fact, head size was even smaller and the lateral line was even less complete than in northern basin *C. bendirei*, thus differences with northern Harney Basin *C. hubbsi* were greater.

Sample sizes were small for Malheur and Snake rivers, but diagnostic characters again followed the pattern from northern Harney Basin. However, prickle counts for *C. bendirei* were more similar to southern Harney Basin ($\bar{x}$=11.8 and 10.1, respectively) than to northern populations ($\bar{x}$=2.2). Other diagnostic characters, head length residuals and lateral line completeness, were not significant (P=0.10 and 0.13, respectively), but did follow the northern Harney Basin pattern with *C. bendirei* having shorter heads and more incomplete lateral lines.

Sample sizes for lower Columbia Basin fish were also small. All fish in the lower basin (Gales Cr. and Clatskanie R.) were *C. bendirei* and most in the upper Willamette tributaries were hybrids. We found no specimens of *C. hubbsi,* which makes the identification of hybrids questionable. As in Snake R. samples, the three diagnostic characters follow the northern Harney Basin patterns, but the two morphological measurements were not significant. More work is required to resolve the taxonomic status of Willamette R. mottled sculpins.

Identification of individuals is not easy and may require drainage-specific criteria. At this stage in our understanding, we believe these species can be diagnosed by the number of prickles on the left side of the body, with *C. bendirei* having less than 30 and *C. hubbsi* more than 90. Hybrids were intermediate. Two additional characters, residuals from the relationship, HL= 0.2238 + 0.3115SL, and completeness of the lateral line, corroborated identifications, with *C. bendirei* having a smaller head and more incomplete lateral line than *C. hubbsi* (Figure 4).

The diagnoses of these forms may apply to Upper Columbia Basin specimens evaluated by Peden et al. (1989). In that study, specimens with prickles present were identified as "nominal *C. bairdi* and (or) *C. hubbsi*" while those with fewer than 10 prickles and smaller heads were identified as "nominal *C. confusus*". The latter characters are consistent with *C. bendirei*. As in this study, the distribution map in Peden et al. (1989) shows that the two species are usually geographically segregated.

Bison and Bond (1971) suggested that many fish in Harney Basin "originated from the basin's Pleistocene connection with Malheur River" and also implicated stream capture between the Silvies and John Day drainages to explain the lower Columbia fish fauna found in central Silvies R. Although their stream capture explanation might apply to other fishes, there is no evidence of *C. bairdi* complex in the John Day drainage and it seems most likely that the presence of these sculpins in Harney Basin preceeded any stream capture involving the John Day drainage. Coexistence of two species in northern Harney Basin, the Malheur R., and possibly the Upper Columbia R. suggests differentiation occurred prior to Pleistocene isolation of Harney Basin. Because Harney Basin had a Pleistocene connection with the Malheur R., the simplest explanation for the pattern is that differentiated species coexisted prior to the Pleistocene isolation of Harney Basin.

Peden et al. (1989) suggest the need to examine characters of *C. bairdi* complex in terms of their relationships to habitat, especially upstream and downstream variants, and in terms of possible hybrid influences from other sculpins. The forms we identified could be ecotypes rather than species. In Harney Basin, *C. bendirei* was most common upstream in smaller or isolated creeks whereas *C. hubbsi* was common in mainstem Silvies R. However, the upstream-downstream pattern did not hold in the Willamette and lower Columbia nor does it appear to hold in the upper Columbia (Peden *et al* 1989). Habitat partitioning is expected of ecotypes as well as closely related species and does not resolve the question. The congruence of morphology and distribution, however, was consistent with two species meeting in narrow hybrid zones. A better understanding of reproductive requirements, morphological differentiation, demographics and genetics of these species especially in contact zones in Silvies and Malheur rivers would greatly increase our understanding of western *C. bairdi* complex.

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Relationships of Remnant Trees to Vascular Undergrowth Communities in the Western Cascades: a Retrospective Approach

Abstract

Managers of federal forests in the U.S. Pacific Northwest are charged with managing timber harvest while maintaining ecosystem functions and biological diversity associated with old, unmanaged forests. Thus, timber-oriented management is being replaced by ecosystem management, which includes leaving live trees (green trees), snags, and coarse woody debris after harvest. We used a retrospective approach to assess potential effects of green-tree retention on vascular undergrowth in the western Cascades of Oregon. Fourteen natural two-storied stands of remnant trees (> 300 yr) over 65-125 yr old regeneration were paired with neighboring stands of the same age but lacking remnants. Species richness and cover of shrubs, all herbs, and late-successional shrubs and herbs did not differ systematically between stands with and without remnant trees. However, communities of herbs and shrubs varied with the percentages (% BA/ha) of Douglas-fir (*Pseudotsuga menziesii)* and western hemlock (*Tsuga heterophylla*) in the regeneration, which varied with remnant densities. Regeneration densities and percentages of western hemlock in the regeneration were positively correlated with remnant tree densities. In contrast, percentages of Douglas-fir in the regeneration and overall conifer volume were negatively correlated with remnant densities. Undergrowth cover and species richness was generally greater in relatively open, Douglas-fir dominated forests, which were associated with physiographically drier sites and fewer remnant trees. Results for these natural, two-storied stands suggest that variable levels of green-tree retention in managed forests may provide for a diversity of undergrowth communities

Introduction

The preservation of biological diversity is one of the most important environmental priorities today (Lubchenco et al. 1991). In the U.S. Pacific Northwest (PNW), concern focuses on loss of biotically rich and structurally complex old-growth forest (FEMAT 1993). These forests provide habitats for many organisms (Norse 1990), whereas stands managed for maximum timber productivity typically have fewer of the structural and compositional features that provide the diversity of habitats on which many species depend (e.g., Alaback 1982, Franklin and Spies 1991, Hansen et al. 1991). Old-growth forests of the PNW are characterized by several structural features, including a multi-layered canopy consisting of living and dead trees and abundant coarse woody debris (Franklin et al. 1981). The mosaic of gaps and shaded areas allows a spatially heterogeneous understory and a rich assemblage of plant species (Franklin and Spies 1991). Some surveys show that management practices that interfere with the development of old-growth structural features may result in a long-term loss of species diversity (e.g., Halpern 1993). Thus, forest managers, who are required to manage for timber production, as well as maintenance or enhancement of ecosystem functions and biological diversity (Kessler et al. 1992; Swanson and Franklin 1992; R.O.D. 1994), are now charged with fostering structural and compositional heterogeneity in forests.

Much of the original old-growth forest area of the Pacific Northwest has been harvested, with a two-thirds decrease in old-growth area over the last five decades (Bolsinger and Waddell 1993). Efforts to protect remaining old-growth stands are important for protection of old-growth associated species, but re-creation of such systems may also be invaluable (R.O.D. 1994). Management techniques may be able to accelerate the development of structural features characteristic of old-growth forests, including large trees over intermediate canopy layers with abundant standing and down coarse woody debris (CWD). Consequently, forest managers are beginning to apply "ecosystem management" techniques in forests within the range

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of the Northern Spotted Owl (*Strix occidentalis*), seeking to re-create structurally diverse stands by carrying through harvest some of the structural legacy of the former stands (e.g. large green trees, CWD, and snags; FEMAT 1993, R.O.D. 1994). These techniques, in part, mimic natural disturbances (e.g., fire), which often leave standing green trees and snags, as well as CWD (Swanson and Franklin 1992). However, these changes are being implemented with little data on long term effects, particularly whether they will enhance biotic diversity or communities characteristic of older forests (but see, Aubry et al. 1999; Halpern et al. 1999).

Unmanaged forests in the western Cascades of Oregon consist of a mosaic of stands that were created and influenced by fires (Morrison and Swanson 1990, Agee 1991) and other disturbances. Past disturbances of diverse intensity and frequency left varying numbers of remnant trees, creating a variety of stand structures. This variation presents the opportunity to examine the relationships of remnant tree carry-over to the structure and composition of resulting stands. Natural, two-storied stands (remnant trees over regeneration) created by fire may be analogous to stands that are being created by ecosystem management techniques, projected into the future. A retrospective approach allows insights into the possible consequences of these techniques without waiting decades for results from newly manipulated stands to become apparent (Swanson and Franklin 1992).

We used a retrospective approach to examine the apparent effects of variations in ecosystem carryover, specifically remnant tree densities, on abundance and species composition of herbs and shrubs in rotation-aged stands (65-125 yr). We assessed whether simple univariate measures, such as species richness or cover, differed systematically between stands with remnant trees and those without remnants. In addition, we analyzed composition of herb and shrub communities, and relationships between those communities and overstory characteristics. The results are important to our basic understanding of influences on undergrowth, which have been little studied in natural two-storied stands of this region (Hansen et al. 1991). (We use the term "undergrowth," rather than "understory" to emphasize that our focus was on herbs and shrubs, with understory trees excluded.) This study also provides important information for forest managers, who need to assess probable consequences of remnant, overstory trees on undergrowth diversity, abundance, and communities. Parallel studies on the same sites examined relationships of remnant trees to growth of conifer regeneration (Zenner 1994; Acker et al. 1998; Zenner et al. 1998) and canopy epiphytic lichens (Peck and McCune 1997).

While our retrospective approach allows us to anticipate some potential effects of logging with green-tree retention on undergrowth, such an approach has limitations. For example, the natural, two-tiered stands that we studied originated after fire, not after timber harvest, which may influence responses. Thus, apparent responses to remnant density may, in fact, be responses to variation in disturbance intensity that led to differential survival of remnant trees. Our approach allows us to assess correlations between undergrowth and overstory characteristics, but our ability to infer causation is limited.

Study Area

This study was conducted on the Willamette National Forest, Oregon, within the *Tsuga heterophylla* (western hemlock) zone (Franklin and Dyrness 1973) of the central western Oregon Cascades at elevations between 520 and 850 m. All sites were within the *Tsuga heterophylla/Berberis nervosa* (TSHE/BENE) and *Tsuga heterophylla/Berberis nervosa-Gaultheria shallon* (TSHE/BENE-GASH) associations (Hemstrom et al. 1987). These plant associations are among the most common in the Willamette National Forest and are similar to one another in that they are typically found at mid-elevations on moderately productive, well-drained sites. We restricted sites to these two associations to minimize among-site environmental variation, although TSHE/BENE sites tend to be more mesic than TSHE/BENE-GASH sites. Stands were sampled on a range of aspects and topographic positions.

Methods

Plot Selection

Natural two-storied stands of mature remnant trees (≥300 yr) over well-stocked rotation-aged regeneration (65-125 yr old) were selected based on suggestions by U.S. Forest Service personnel and on field inspection. Remnant trees are those that were dominant or co-dominant at the time of the

regeneration-initiating disturbance. We reduced inter-stand heterogeneity by choosing only stands that appeared to originate after wildfire (e.g., fire scars on remnants), rejecting stands originating after other disturbances, such as wind storms or selective harvesting. To maximize our ability to infer effects potentially attributable to remnant trees (as opposed to those attributable to abiotic variables), we paired study plots: one plot with remnant trees (3 - 57 trees per ha) paired with a plot without remnants. Thus, each site had to be large enough (1-2 ha) to include two areas; one with remnants (remnant megaplot) and one without remnants (non-remnant megaplot). Edges of megaplot pair members were 5 - 50 m apart. Edge effects resulting from proximity to clearcuts were minimized by locating sites at least 20 m, and generally much farther, from the edge of a clearcut. Final sample size was 14 pairs of plots. All sites were sampled between late June and early September, 1993.

Plot Design

On each site, trees, herbs and shrubs were measured within a pair of nested, concentric, fixed-radius plots (Figure 1). Remnant trees and aspects of the physical environment were measured in the largest circular plots ("megaplots," 30.9 m radius, area = 3000 m^2). Tree regeneration, herbs, and shrubs were measured in smaller "detection plots" (radius = 12.62 m, area = 500 m^2, Figure 1), which were centered within megaplots (one per megaplot). (Detection plots were so-named, as they were the areas in which undergrowth was measured to detect potential remnant effects.) Sampled areas within remnant and non-remnant plots were separated by at least 30 m, a distance over which remnant effects on regeneration are likely to be minimal (Hoyer 1993). Sparse remnant trees may influence regeneration or undergrowth, yet may be missed in smaller plots (such as the detection plot); measurement of remnants in the larger megaplot minimized this potential problem. Within detection plots, 10 subplots (radius = 2 m) were randomly placed, each with three microplots (0.2 x 0.5 m) for a total of 30 microplots per detection plot (Figure 1).

Plot Measurements

Megaplots

Slope, aspect, physiographic class, coarse woody debris and remnants were measured or recorded

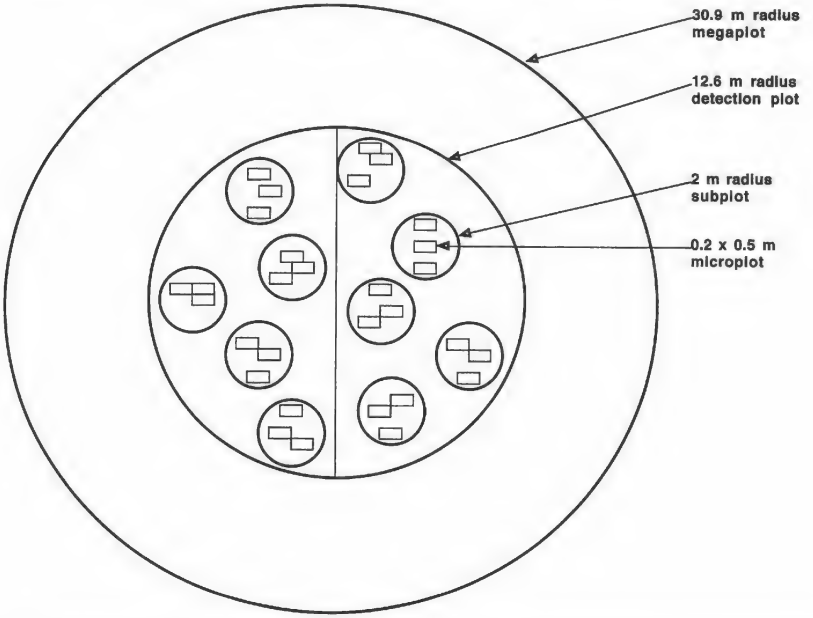

Figure 1. Sampling schematic, showing shrub subplots and herb microplots within the detection plot portion of the megaplot. A pair of such megaplots was established at each of the 14 sites.

in the megaplots as follows. Physiographic classes were based on aspect and topographic position, ranked to reflect increasing potential moisture status as influenced by these factors (1 = W, SW, S facing middle/upper slopes; 2 = SE, NW facing middle/upper slopes; 3 = N,NE, E facing middle/upper slopes; modified from Kessell 1979; Rose 1994). For each remnant tree, we recorded species, diameter at breast height (dbh), height, and two perpendicular crown radii. Ages of most remnants were determined from increment cores taken at breast height. The post-disturbance stand had been affected not only by current remnants, but also by remnants that died over its history. Thus, dead remnant trees were assigned to a decay class (Bartels et al. 1985; Neitro et al. 1985) and measured variously depending on decay class. Trees of decay classes 1, 2 and 3 (class 1 being least decayed) were measured in the same way as live remnants when possible, including the extraction of increment cores (for methods, see Zenner 1994). Remnants in more advanced decay classes were excluded from remnant tree analyses, on the assumption that they were dead throughout the post-disturbance stand's history (Acker et al. 1998). The following remnant tree variables were then calculated: density (trees/ha), total basal area at time of stand initiation (henceforth, total BA; m^2/ha), live BA (m^2/ha), live volume (m^3/ha), and live crown area (m^2/ha) (see Acker et al. 1998 and Zenner et al. 1998 for calculations and rationale).

Detection Plots

We measured species and dbh of all trees (dbh ≥ 20 cm) in detection plots and calculated density, BA, species composition (percent of BA) and volume of conifers and hardwoods in the post-disturbance stand (Zenner 1994). Coarse woody debris and snags (diameter ≥ 10 cm) were measured, and number (no./ha), volume, and cover or basal area were determined (for methods see Zenner et al. 1998).

Species richness of shrubs and herbs in detection plots was based on measurements in subplots and microplots (see below) and a 30 min ocular inspection of each detection plot. The time-constrained ocular inspection was intended to increase the species lists over those based on sub- and microplot sampling, yet maintain consistency in sampling intensity across sites.

Sub- and Microplots

Shrub cover was estimated in subplots (2 m radius) using a modified Daubenmire cover-class scale which approximates an arcsine squareroot transformation (1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = 75-95%, 7 = 95-99%, 8 = >99%; Muir and McCune, 1988). Shrubs were defined structurally as all vascular species > 0.5 m and < 3 m in height. Herbaceous plants taller than 0.5 m (e.g., *Polystichum munitum* and *Pteridium aquilinum*) were included with shrubs because their influences on the herb stratum (e.g., light interception) may be similar to those of shrubs. Because some species were in both herb and shrub strata, as defined by height, a given species may be represented in both layers for a plot.

We measured tree canopy cover (subcanopy and canopy trees combined, but excluding tall shrubs such as *Acer circinatum*) using a convex spherical densiometer. We took readings in the four ordinal directions from the center of each subplot ("wedge method"; Strickler 1959). The densiometer was fastened and leveled at 1.1 m above the ground on a pole at plotcenter. Canopy cover values for each subplot were averaged to give detection plot-level estimates of cover.

Herb cover was estimated in microplots (0.2 x 0.5 m) using the cover-class scale used for shrubs. All vascular plants ≤ 0.5 m tall were considered "herbs." Nomenclature follows Hitchcock and Cronquist (1973).

Data Analysis

Data on shrubs and herbs were analyzed separately. Cover data were aggregated to the detection plot level by summing across subplots and microplots. Henceforth, "plot" refers to detection plots for tree regeneration, CWD, herbs, and shrubs and to megaplots for remnant trees (live and dead). Cover-class values were used in most analyses, rather than back-transforming to mid-points of cover-class percentages, because cover-class scores improve statistical properties of the data by approximating an arcsine squareroot transformation. We used SPSS/PC+ Version 4.0 (Norusis/SPSS Inc. 1988) for univariate analyses and PC-ORD (McCune 1993) for multivariate analyses.

We tested whether remnant and nonremnant plots differed in shrub and herb cover and species richness, using comparisons of means and

standard errors. We also tested whether richness of species considered to be late-successional (FEMAT 1993) differed between remnant and nonremnant plots. Late-successional species included *Achlys triphylla, Adenocaulon bicolor, Anemone deltoidea, Chimaphila menziesii, C. umbellata, Coptis laciniata, Corallorhiza maculata, C. mertansiana, Disporum hookeri, Goodyera oblongifolia, Hypopitys monotropa, Monotropa uniflora, Pyrola picta, Trillium ovatum, Vaccinium parvifolium, Vancouveria hexandra, and Whipplea modesta.* We tested whether species richness or cover of all herbs and of late-successional herbs was correlated with overstory attributes, using Spearman's rank correlation.

To describe and interpret species compositional patterns and their relationships to site variables, we analyzed the species cover data using nonmetric multidimensional scaling ordination (NMS; Kruskal 1964; Mather 1976) with a Sorenson distance measure for each layer (shrub and herb) and for late-successional species. Outliers were plots whose average distances were greater than 2.5 standard deviations from the mean distance; two such plots were omitted. We examined correlations of environmental variables with ordination axes, using Pearson's r and overlays of environmental variables on ordination diagrams. We rotated axes by 15° for shrub ordinations to maximize the variance of important environmental variables (variables with the highest r^2) along them (McCune 1993). Apparently strong relationships between individual species and environmental variables (suggested by overlays of environmental variables on ordination diagrams and correlation coefficients ≥ 0.3) were then analyzed directly using Pearson correlations, as were correlations among environmental variables. Because we made multiple comparisons, probabilities associated with correlation coefficients should be interpreted with caution.

Results

Relationships Among the Remnant Trees, the Regeneration Cohort and Environmental Variables

Remnant tree density in megaplots ranged from 3 to 57 trees/ha, (live remnants only) with an average of 21 remnants per hectare. Density of all live trees (remnants + regeneration) ranged from 440 to 1920 trees/ha and averaged 894 trees/ha (see Zenner et al. 1998 for a complete listing of overstory characteristics in remnant and nonremnant plots). Canopy cover percentages were always > 92% and averaged 96%. All remnant tree attributes (total BA [at time of stand initiation], live BA, total volume, crown area) were highly inter-correlated ($P \leq 0.01$, minimum r = 0.38; see Zenner et al. 1998, for details). As remnant density increased, percentages of western hemlock (% BA/ha) generally increased, and percentages of Douglas-fir and overall conifer volume (m^3/ha) decreased (Pearson's r = 0.61, -0.62, and -0.67 respectively; all $P \leq 0.01$).

The characteristics of the regeneration cohort of trees were also interrelated. Canopy cover (including remnants and regeneration trees) was positively correlated with the percentage of western hemlock and negatively correlated with the percentage of Douglas-fir in stands (% BA/ha basis; r = 0.39 and –0.39, respectively, $P \leq 0.05$). Regeneration conifer volume was positively correlated with the percentage of Douglas-fir and negatively correlated with the percentage of western hemlock in stands (r = 0.52 and -0.50, respectively; $P \leq 0.05$), consistent with Rose (1994) and Rose and Muir (1997). In contrast to results for regeneration volume, regeneration density was positively correlated with the percentage of western hemlock in the regeneration (r = 0.32), implying an abundance of relatively small stems in stands with regeneration dominated by western hemlock, a result consistent with others (e.g., Edmonds et al. 1993). Regeneration density was negatively correlated with the cover of CWD (r =-0.39; $P \leq 0.05$).

Abiotic site characteristics were correlated with regeneration characteristics as well. Conifer volume generally decreased as elevation increased (r = -0.39; $P \leq 0.05$), probably reflecting a decrease in the relative abundance of Douglas-fir at higher elevations. Conifer volume was also lower on steeper slopes (r = -0.50; $P \leq 0.05$), but regeneration density increased with slope steepness (r = 0.49; $P \leq 0.05$). Canopy cover and relative abundance of western hemlock (% BA/ha) were positively correlated with physiographic conditions (1 [relatively xeric] – 3 [relatively mesic]; r = 0.52 and 0.73, respectively, $P \leq 0.05$), whereas the relative abundance of Douglas-fir was negatively correlated with physiographic moisture status (r = -0.74, $P < 0.05$).

Relationships of Communities to Overstory and Environment

No systematic differences in herb or shrub cover, or in species richness of herbs, shrubs or late-successional species were detected between remnant and nonremnant plots (Traut 1994). Further, the paired plots did not separate into groups (remnant vs. non-remnant plots) on community ordinations. However, communities did vary along gradients that were related to remnant trees, hence we focus on patterns across all plots, rather than on differences between plot pairs.

Shrubs

We found a total of 24 shrub species across all plots, with a mean alpha diversity of 8.4 species per plot. Multivariate analyses revealed relationships of remnant trees to shrub communities (Table 1). Cover of 8 of the 24 shrub species increased along the first NMS ordination axis, while remnant trees (remnant density, total and live BA, volume, and crown area) decreased (R^2 for Axis 1 = 0.36). Percentages of western hemlock in the regeneration and regeneration density also decreased along Axis 1. In contrast, the percentage of Douglas-fir in the regeneration and overall conifer volume increased along this axis (Table 1). The only abiotic environmental variable correlated ($P \leq 0.05$) with Axis 1 was slope steepness, which increased as remnants increased and as cover by most shrub species decreased. Stands with greater numbers of remnants tended to be at higher elevations, although the correlation of elevation with Axis 1 (r = -0.31) was not statistically significant at $P \leq 0.05$. While several shrub species were strongly correlated with the second ordination axis, it was not related to overstory or measured abiotic site variables (Table 1; R^2 for Axis 2 = 0.32).

TABLE 1. Pearson correlations (r) of shrubs, remnant and regenerating trees, and environmental variables with ordination axes (NMS). Only correlations ≥ ± 0.37 ($P \leq 0.05$) with one or more axes are shown.

Species/Variable	Axis 1	Axis 2
Shrubs		
Acer circinatum	-0.34	0.70
Acer macrophyllum	0.57	-0.35
Castanopsis chrysophylla	0.43	-0.36
Gaultheria shallon	0.78	-0.54
Polystichum munitum	0.07	0.51
Pteridium aquilinum	0.66	-0.22
Rhododendron macrophyllum	-0.02	-0.47
Rosa gymnocarpa	0.55	-0.19
Rubus ursinus	0.80	-0.28
Symphoricarpos mollis	0.56	-0.23
Tsuga heterophylla	0.43	-0.09
Summed cover of shrub species	0.07	-0.97
Remnant and Regenerating Trees, Environmental Variables		
Remnant density (trees/ha)	-0.53	-0.18
Remnant BA (total; m^2/ha)	-0.48	-0.05
Remnant BA (live, m^2/ha)	-0.44	-0.03
Remnant volume (m^3/ha)	-0.39	-0.03
Remnant crown area (m^2/ha)	-0.38	0.00
Tsuga heterophylla regeneration (% BA)	-0.43	-0.23
Pseudotsuga menziesii regeneration (% BA)	0.46	0.23
Regeneration conifer volume (m^3/ha)	0.56	0.05
Regeneration density (trees/ha)	-0.38	-0.15
Slope (%)	-0.40	0.07

Herbs

We found a total of 52 herb species across all plots, with a mean alpha diversity of 10.1 species per plot. Variation in herb communities was predominantly accounted for by the second axis of the herb ordination (R^2 for Axis 2 = 0.52), which was most strongly related to relative abundances of Douglas-fir and western hemlock in the regeneration (Table 2). Correlations of remnant tree attributes with this second axis of herb ordinations were suggestive, but not statistically significant (maximum r = 0.34 [remnant density]; $0.05 < P < 0.1$). While weaker, these correlations were similar to those for shrub communities, in that cover of several herb species was negatively correlated with remnant attributes and positively correlated with the relative abundance of Douglas-fir. Summed cover across herb species and cover by 10 of the 52 individual species was negatively correlated with this axis ($P \leq 0.05$), as was the percentage of Douglas-fir in the regeneration. *Polystichum munitum* was the only herb species that was positively correlated with this axis. Herb community composition also varied along another axis (Axis 1, $R^2 = 0.29$), and several species were strongly correlated with this gradient. However, Axis 1 was only weakly related to overstory variables (maximum r = 0.30 for regeneration volume), and slope was the only abiotic site variable with which it was correlated.

TABLE 2. Pearson correlations (r) of herbs, regenerating trees, and environmental variables with ordination axes (NMS). Only correlations $\geq \pm 0.37$ ($P \leq 0.05$) with one or more axes are shown.

Species/Variable	Axis 1	Axis 2
Herbs		
Acer macrophyllum	0.57	-0.35
Achlys triphylla	0.26	-0.45
Amelanchier alnifolia	-0.57	0.15
Berberis nervosa	0.21	-0.80
Calypso bulbosa	-0.38	0.00
Collomia heterophylla	-0.47	0.07
Galium triflorum	-0.42	0.05
Gaultheria shallon	0.70	-0.59
Linnaea borealis	0.22	-0.45
Polystichum munitum	-0.06	0.62
Pteridium aquilinum	0.49	-0.35
Pyrola asarifolia	0.33	-0.37
Rosa gymnocarpa	0.32	-0.53
Rubus ursinus	0.52	-0.55
Symphoricarpos mollis	0.34	-0.47
Synthris reniformis	-0.57	0.15
Viola sempervirens	0.16	-0.38
Whipplea modesta	0.13	-0.46
Summed cover across herb species	-0.01	-0.89
Regenerating Trees and Environmental Variables		
Pseudotsuga menziesii regeneration (% BA)	0.12	-0.71
Tsuga heterophylla regeneration (% BA)	-0.09	0.69
Slope (%)	-0.39	0.15

TABLE 3. Pearson correlations (r) of late-successional species, remnant and regenerating trees, and environmental variables with ordination axes (NMS). Only correlations $\geq \pm 0.37$ ($P \leq 0.05$) with one or more axes are shown.

Species/Variable	Axis 1	Axis 2
Species		
Achlys triphylla	0.38	0.09
Adenocaulon bicolor	0.42	0.16
Allotropa virgata	-0.07	0.51
Anemone deltoidea	0.77	0.08
Chimaphila menziesii	0.62	0.54
Chimaphila umbellata	0.30	0.55
Coptis laciniata	0.13	0.69
Corallorhiza maculata	-0.49	-0.16
Corallorhiza mertensiana	-0.42	-0.13
Disporum hookeri	0.16	-0.37
Goodyera oblongifolia	0.32	-0.39
Hypopitys monotropa	-0.42	-0.03
Monotropa uniflora	-0.18	-0.41
Pyrola picta	-0.02	0.61
Trillium ovatum	-0.19	-0.63
Vaccinium parvifolium	-0.42	0.07
Vancouveria hexandra	0.47	0.00
Whipplea modesta	0.75	0.06
Remnant and Regenerating Trees		
Canopy cover (%)	-0.64	-0.03
CWD cover (%)	-0.42	-0.29
CWD volume (m^3/ha)	-0.37	-0.30
Regeneration density (trees/ha)	0.02	0.38
Environmental Variables		
Elevation (m)	0.17	0.46

Late-successional species

Multivariate analysis revealed relationships of late-successional species' (FEMAT 1993; see Methods) communities to canopy cover, abundance of CWD, regeneration tree density, and elevation (Table 3). As for ordinations involving all herb species, remnant tree variables were not directly related to either ordination axis. However, by contrast with results for shrubs and all herb species, percentages of western hemlock and Douglas-fir in the regeneration were not directly correlated with the axes of variation in late-successional herb communities (maximum r = 0.29).

The first axis of this ordination was most strongly related to canopy cover and CWD cover and volume, which were negatively correlated with this axis (R^2 for Axis 1 = 0.27). Relatively open plots (lower canopy cover) generally contained *Achlys triphylla, Adenocaulon bicolor, Anemone deltoidea, Chimaphila menziesii, Vancouveria hexandra,* and *Whipplea modesta.* Plots with greater canopy cover and abundance of CWD were typified by the presence of *Vaccinium parvifolium, Corallorhiza maculata, C. mertensiana,* and *Hypopitys monotropa.*

The second axis of the ordination of late-successional species' communities was most strongly related to elevation, with *Allotropa virgata, Chimaphila menziesii, Chimaphila umbellata, Coptis laciniata,* and *Pyrola picta* typical of plots at higher elevations (R^2 for Axis 2 = 0.24). Regeneration density also increased with elevation along this axis.

Species richness

The most species-rich plots tended to have higher percentages of Douglas-fir relative to western hemlock in the regeneration and more open canopies (Table 4). These plots also tended to be

TABLE 4. Correlations between herbaceous species richness and environmental variables (Spearman's correlation coefficients; probabilities are ≤ 0.05 except where indicated). % PSME and % TSHE are percentages of *Pseudotsuga menziesii* and *Tsuga heterophylla*, respectively, on a basal area basis; physiographic classes were ranked, with 1 = driest and 3 = moistest, as indicated by slope, aspect, and topographic position; "late-successional" species are based on FEMAT (1993).

Richness Component	Canopy Cover (%)	% PSME	% TSHE	Physiographic Class
All Herbaceous Species	-0.56	0.72	-0.74	-0.55
Late-successional Species	-0.38	0.48	-0.48	-0.27[ns]

[ns] = $P > 0.05$

physiographically drier. Patterns in species richness for late-successional species paralleled those for all herb species, in that richness increased with the relative abundance of Douglas-fir and decreased with the relative abundance of western hemlock. Correlations of late-successional herb species richness with overstory attributes were weaker than were correlations of those attributes with richness across all herb species (Table 4).

Summary and Discussion

Species Richness and Cover

We had anticipated that species richness or cover, particularly for late-successional species, might be higher in remnant than in non-remnant plots. For example, remnant trees might ameliorate site conditions after disturbance, potentially enhancing survival or establishment of herb and shrub species in the years immediately following the disturbance. In addition, remnant survival suggests that the regeneration-initiating disturbances (in the case of our plots, fires) were less intense in remnant than in nonremnant plots. Lower intensity disturbances might be expected to enhance post-disturbance survival of undergrowth species. The lack of systematic pairwise differences between remnant and nonremnant plots in species richness or cover that we found could result from several factors, including: (1) pre-disturbance differences in species composition or abundance that persisted through the disturbance via survival of roots, rhizomes or seeds; (2) effects of remnants on density and species composition of regenerating trees, whose effects on undergrowth may have obscured direct remnant or disturbance-intensity effects (see below); or (3) other site-to-site differences that overwhelmed remnant or disturbance-intensity effects on undergrowth. Our retrospective approach does not allow us to distinguish between these, or other, influences.

Shrub and Herb Communities

Analyses of herb and shrub communities suggested, however, that remnant trees may have influenced their development, at least indirectly. While remnant density or basal area itself was not always correlated with axes of variation in shrub and herb communities, remnant characteristics were generally correlated with composition and density of the regeneration trees, which were, in turn, strongly related to the undergrowth communities.

For example, major axes of variation in shrub and herb communities were always correlated with the relative abundance of Douglas-fir and western hemlock in the regeneration, or with density of regeneration trees. Further, cover by several individual herb and shrub species decreased as the relative abundance of western hemlock increased. Relative abundance of western hemlock and density of regeneration trees was higher when remnant density (or BA) was higher, while relative abundance of Douglas-fir in the regeneration was generally higher when remnants were sparser. Shadier conditions associated with remnant trees may have enhanced the relative success of western hemlock compared to Douglas-fir on remnant plots, as western hemlock is more shade-tolerant than Douglas fir (Burns and Honkala 1990). The relative abundance of Douglas-fir also tended to be higher on physiographically drier sites, which supported lower remnant densities. Physiographically drier conditions on sites with lower remnant densities may have been more suitable for Douglas-fir than for the relatively moisture-demanding western hemlock.

The inverse relationship of cover by several shrub species to remnant density, BA, volume and crown area may have been mediated by the relative abundance of western hemlock regeneration. Overstory influences could act via the canopy (e.g., light or moisture interception), the soil (e.g., litter chemistry and accumulation), or both. Western hemlock and Douglas-fir have different influences on the understory environment (e.g., Alaback 1982, Stewart 1986). For example, less

direct light comes through relatively dense hemlock canopies than through those of Douglas-fir (Stewart 1986, 1988) and therefore, greater development of many shrub species often occurs under Douglas-fir than under western hemlock. In addition, sunflecks, which can be important to many understory species (Pearcy 1983), may be more frequent under Douglas-fir than under western hemlock (Antos and Zobel 1984). We found that cover of *Gaultheria shallon* and *Acer circinatum* was negatively correlated with the relative abundance of western hemlock ($r = -0.46$ for both; $P \leq 0.05$). Both *G. shallon* and *A. circinatum* are sensitive to overstory density, and often show increased growth in thinned stands (Tappeiner and Zasada 1993). *Gaultheria shallon*, although not highly shade-tolerant, may do well under a uniform, somewhat open canopy (Messier 1992), as is often found in stands dominated by Douglas-fir. With regard to *A. circinatum,* Anderson (1967) found a positive correlation between its density and basal area of Douglas-fir within the stand, and Stewart (1986) found that it was more commonly present in stands dominated by Douglas-fir than in those dominated by western hemlock, consistent with our findings. Of course, Douglas-fir and western hemlock have differential effects on site factors in addition to light, such as moisture interception (e.g., Voigt 1960, Rothacher 1963) and litter chemistry, and these differences may also have influenced shrub communities..

Several herb species that were negatively correlated with the relative abundance of western hemlock (based on the ordination of herb communities), and thus positively correlated with the relative abundance of Douglas-fir, are typical of drier sites (e.g. *G. shallon*, *Whipplea modesta*, *Linnaea borealis*; Zobel et al. 1976; Gagnon and Bradfield 1986). Hence, differences among sites in moisture status as well as differences in light regime may have been influential. Relationships of undergrowth communities to physiographic moisture status were also suggested by overlays of physiographic classes on an ordination of herb and shrub communities together, which revealed that plots with lower shrub and herb cover tended to be physiographically moister (Traut 1994). The negative correlation between herb species richness and physiognomic moisture status that we observed is consistent with results from other studies of forests in the region, which have found that species richness often is higher in relatively dry forest communities (e.g., Zobel et al. 1976). There were some exceptions to the generally lower cover on physiographically-moister sites, however, such as *Coptis laciniata*, which commonly indicates moist sites (Hemstrom et al. 1987), and which was more abundant in western hemlock-dominated sites. Because physiographically moister sites supported more remnants and more western hemlock in the regeneration, we are unable to separate potential physiographic influences on undergrowth communities from influences mediated by overstory composition (including remnants), however it is likely that both types of influences are important. (Note that we did not measure soil moisture status directly.)

Three of the late-successional species characterizing plots with relatively high canopy and CWD cover were mycotrophs (*Corallorhiza maculata, C. mertensiana* and *Hypopitys monotropa;* Hitchcock and Cronquist 1973, Furman and Trappe 1971). Logs may help to maintain mycorrhizal associates of these species through stand-initiating disturbances and in post-disturbance stands (Spies et al. 1988). The mycorrhizae associated with *H. monotropa* are compatible with western hemlock (Furman and Trappe 1971), the most abundant conifer in stands with higher canopy and CWD cover. Coarse woody debris also provides a favorable substrate for many non-mycotrophic species (Stewart 1986), such as *Vaccinium parvifolium*, which occurred commonly on logs, and whose cover was associated with relatively abundant CWD. Finally, CWD may also influence soil moisture and stand humidity (Franklin et al. 1981). Coarse woody debris can retain water throughout the summer and also provide shade and diminished wind at the forest floor, thereby reducing evaporation. We found that two species often associated with mesic sites, *Trillium ovatum* and *Polystichum munitum* (Hitchcock and Cronquist 1973), tended to be more abundant in plots with more CWD.

Herbaceous species richness and abundance often decrease with canopy closure (e.g., Alaback 1984; Stewart 1988; Oliver and Larsen 1990; Duffy and Meier 1992), and the communities that we studied were probably affected variously by this stage in stand development. All of our sites had apparently advanced to or through the self-thinning (Drew and Flewelling 1979) or stem-exclusion (Oliver and Larson 1990) phase (Zenner et

al. 1998). However, the effects of this stage on the undergrowth were probably more intense in the relatively dense, hemlock-dominated stands than in the stands dominated by Douglas-fir, with their relatively open canopies. In extreme cases, all herbaceous plants may die under dense stands of western hemlock (Alaback 1982). Another sampling of these stands in the future, when the undergrowth has recovered further from canopy closure, might result in different interpretations of relationships between remnant trees and undergrowth than those offered here; the longevity of shade-tolerant herbs during the stem-exclusion stage is not well-understood (North et al. 1996).

Answers to questions about the influence of remnant, overstory trees on undergrowth communities are important but difficult to find, because these new forest management techniques are only now being implemented (Aubry et al. 1999; Halpern et al. 1999). Retrospective studies such as this can, however, help us to understand and predict potential long-term consequences of these techniques (Swanson and Franklin 1992). Long-term consequences may differ substantially from those that would be predicted based on study over shorter time periods. For example, a study that assessed initial (16 month) responses of understory plant diversity to a green-tree retention harvest found that herb and shrub species richness and evenness were significantly higher in the green-tree retention cut than in an adjacent clearcut and an intact 65-yr old forest (North et al. 1996). Further, cover by shade-tolerant plants was greater in the retention cut than in the clearcut. Our results suggest that such early differences in undergrowth between green-tree retention cuts, clearcuts, and intact forests might not persist. Studies of species' attributes likely to affect survival, re-establishment, and reproduction under alternative forest management scenarios are needed, as are long-term monitoring studies to follow consequences of such management practices (see Halpern et al. 1999).

Limitations in the analogy between our natural, two-tiered stands and those that will result from timber harvesting with green-tree retention must be borne in mind. For example, harvesting will not always be followed by burning, while the regeneration in our sites was initiated after fires. It is unclear to what extent the absence of fire in managed stands will affect their successional trajectories compared to those followed in natural, fire-origin stands. How will planting of trees in particular densities and species mixtures in managed stands affect undergrowth compared to effects apparently associated with natural regeneration, as occurred on our sites? Will the spatial pattern of green-tree retention (aggregated versus clumped, for example) affect responses in the undergrowth? Despite these limitations, our study does provide some insights for forest managers and ecologists on potential effects of green-tree retention on undergrowth communities.

Our results underscore the importance of defining management goals. We suggest that if the goal is simply to foster high vascular species richness and cover, then stands with relatively open canopies, higher percentages of Douglas-fir, and fewer remnant trees might be favored. However, if goals include provision of habitats suitable for a wide range of plant communities, then retention of variable numbers of remnant trees may be desirable. The potential importance of retaining remnant trees is substantiated by a parallel study (conducted in the same plots as those used here), which reported that biomass of alectorioid and cyanolichens, both often associated with older forests, was greater in plots with remnant trees than in those lacking remnants at low elevations (Peck and McCune 1998). Our results also reinforce the importance of CWD as an important habitat component.

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Relative Humidity Gradients Across Riparian Areas in Eastern Oregon and Washington Forests

Abstract

Riparian relative humidity gradients were examined at twelve sites east of the Cascade Mountains in Oregon and Washington in 1997. Relative humidity was monitored at increasing distances from stream edge to 30 m in the adjacent forested stands. Within 10 m of stream edge relative humidity was similar to upland conditions with little change beyond 10 m. In 9 of the 12 sites differences in mean minimum relative humidity were significant ($P < 0.05$) between 0 and 5 m. The length of time that relative humidity was less than 50% between 0 and 5 m was significant at 11 of the 12 sites. Diurnal fluctuations ranges of more than 75% RH with maximums close to 100% occurred at night at all sites. The diurnal pattern of temperature is the dominant process in air moisture regime in these eastside forests. The small daytime increases in relative humidity close to the stream, which can be maintained over short distances by steep local topography, are apparently due to evaporation from wetted stream width and transpiration from vegetation immediately adjacent to the stream.

Introduction

Aquatic communities and adjacent riparian communities are ecologically interwoven. Riparian sources of nutrients are the starting block for many aquatic food chains and emerging insects and fish are food sources for terrestrial fauna (Meehan, 1996). Nutrients from stream sources, such as salmon carcasses, have been demonstrated to move through both aquatic and riparian pathways (Bilby et al. 1998, and Wipfli 1997). Some animals (insects and amphibians) have both aquatic and terrestrial life history stages. These habitats in and around streams are unique in forested landscapes, and support diverse and specialized flora and fauna. Many of these riparian specialists are dependent on the higher amounts of moisture that are available close to streams. These include vascular plants that are moisture obligates, amphibians whose skin needs to be moist, and non-vascular plants that acquire moisture from the atmosphere. The higher moisture levels found in riparian areas are prerequisite for the survival of these organisms.

The water in the stream channel, beneath the channel in the hyporheos, and en route to the channel through various groundwater pathways, all contribute to the available moisture in riparian zone. These sources of soil moisture are utilized by vegetation, and indirectly enter the atmosphere via transpiration and directly by surface evaporation. Evaporation from the stream surface is a source of local air moisture. Perhaps it is only an important contributor when dry conditions prevail within the surrounding riparian areas, since both evaporation from terrestrial surfaces and transpiration by upland vegetation will be reduced during periods of high temperature and infrequent precipitation that are common during summer in eastern Oregon and Washington.

Prior to the early 1990's, the investigation of microclimate characteristics in forested landscapes was rare. Plant physiology work was done to examine moisture levels with respect to its impact on limiting growth (Hoffman 1973) in mostly agricultural settings. Others (McCaughey et al. 1997) examined microclimate influence within different forest types with those results being applied to tree growth. Chen et al. (1995) completed a study on the westside of the Cascades in the Puget Sound area focusing on the microclimate gradients from the edge of recent clear-cuts into "old-growth" timber stands. While none of the research focused on riparian areas, others have recently begun investigating riparian microclimate gradients. In western Washington (Brosofske et al. 1996) and northern California (Ledwith 1996) studies were conducted of riparian forests dominated by stands of Douglas fir with annual rainfall of 150 cm. or more and adjacent to clear-cuts. While these studies did examine microclimate gradients in riparian areas, those forest stands are unlike the forests dominated by Ponderosa pine

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of the eastside of the cascades. East of Cascades in OR and WA there are much lower amounts of annual precipitation (< 50 cm) and the timber harvest approaches usually do not include clearcutting.

The purpose of this investigation was to analyze relative humidity gradients within riparian areas and adjacent uplands across a variety of eastern Oregon and Washington conditions. All sites were on commercial timber lands, with selective harvest (partial harvest) as the silvicultural prescription. This information is necessary to prescribe effective buffers for riparian dependant flora and fauna of eastside forests. The gradients of relative humidity were studied during the dry and hot conditions that prevail in eastern Oregon and Washington during mid-summer.

Two metrics of relative humidity (RH) calculated daily were used to examine the potential biological effects of relative humidity gradients in eastside forests: minimum relative humidity and length of time (hrs) less than 50% RH. Minimum relative humidity reflects the extreme conditions, since maximum RH approaches saturation (100%) every night. The second metric, the length of time relative humidity was less than fifty percent, was chosen as a measure of length of potential exposure of moisture obligate flora and fauna to low RH levels. The gradients of these metrics from streamside to the adjacent upland forest were examined.

Methods

Relative humidity gradients were examined at 12 sites in Washington and Oregon. The twelve sites were distributed in the Teanaway (WA), Klickitat (WA), and Grande Ronde (OR) watersheds (Figure 1). At these sites there was no measurable

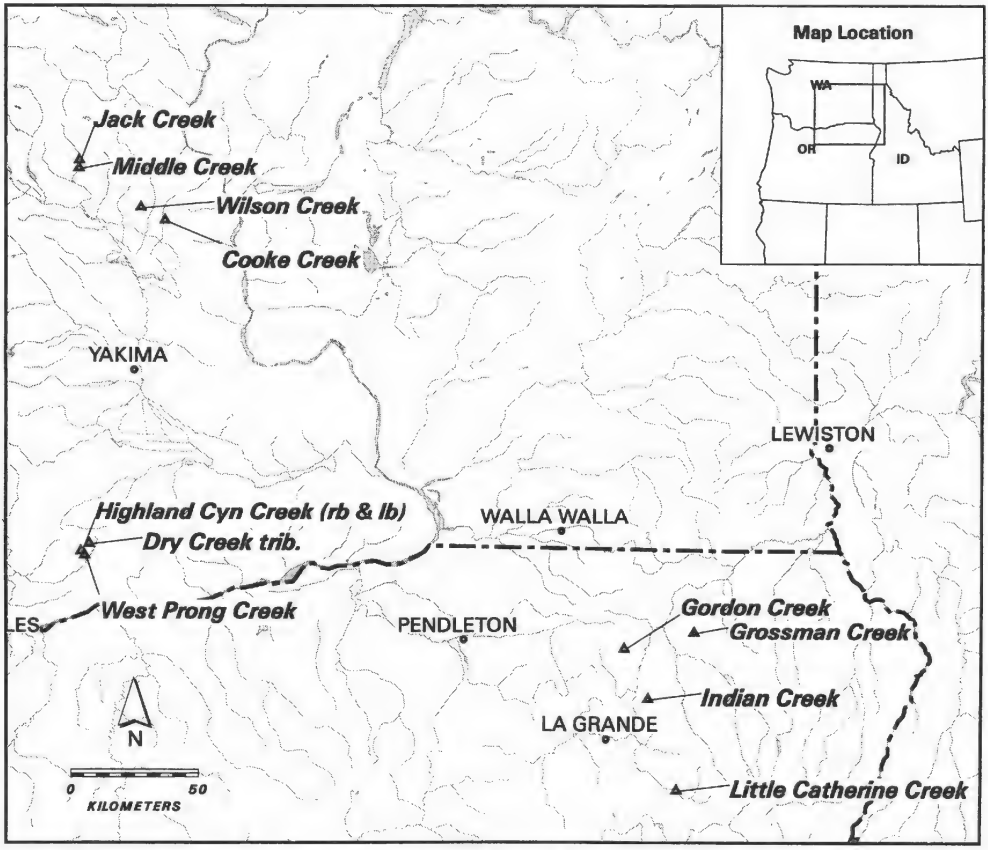

Figure 1. Twelve microclimate study sites east of the Cascade Range in Washington and Oregon.

precipitation for two days prior to or during the study. At each site an array of relative humidity data recorders (Onset Computer Corp. Hobo-RH) were set up for five to nine days between 17 July and 12 August 1997. This time frame was selected because of the expected dry and hot climate. Each array consisted of 12 transect points (Figure 2), with three each at streamside, 5 m and 10 m from stream edge. Single transect points were placed at 20 and 30 m as well as a control in a nearby opening. The array was placed randomly within a reach, after the reach had been examined for potential confounding factors such as roads, trails or landings. The transect points at 20 and 30 m followed a straight line with the middle points from the other distances. The instrument set in the opening served as control, being beyond any direct stream influence or shade. All instruments were 0.5 m above the ground surface and shielded from direct sunlight, without impedance of airflow. Pilot work had found the daily maxima and minima values to occur over a short time interval. Therefore all monitors recorded RH at ten minute intervals; with this interval the absolutes could only be missed by five minutes. Estimates of air temperature maximums were from local meteorological stations in La Grande, OR for Grande Ronde sites, Ellensburg, WA for Teanaway sites, and Goldendale, WA for Klickitat sites.

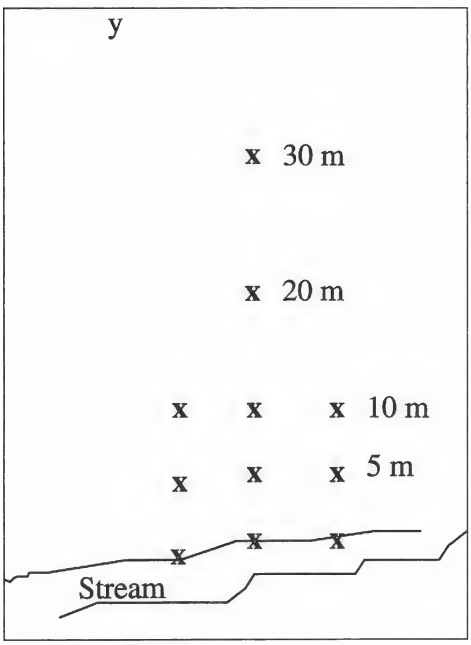

Figure 2. Instrument layout of transects with three replicates at 0, 5, 10 m and transect points at 20 and 30 m. Transect lines are 5 m apart. Y (control) is a site in an opening with minimal shade and more than 30 m from the stream.

At each site, reach and transect data were collected. Stream channel grade was measured with a hand-held clinometer and a mean stream wet width was calculated from 3 measurements. At each transect point percent shade and basal area were measured. Percent shade was calculated from the mean of four shade measurements, one in each compass direction, made with a hand-held concave densiometer. Basal area was measured with a 10 x prism 360^0 at each transect point. Tree size distribution was divided into five classes: 0–10, 10–20, 20–40 and >40 cm dbh. The understory coverage in three categories (% grass cover, shrub volume and tree branch volume) was estimated with a 1 m by 0.5 m cylinder at each transect point. The percent of each category found within the cylinder was estimated as the volume of vegetation found in each quadrant and summing the quadrants to estimate percent occupance by volume. Site characteristics, percent shade and basal area (ft^2/ac), were regressed against mean minimum relative humidity at each site for all transect points. Local topography was measured between transect points with a hand-held clinometer.

Quality assurance and control protocols of the instruments included before and after QC checks and a single set of duplicates at each site. Quality control checks of relative humidity instruments were placed within an enclosed space of water saturated air above a sodium chloride solution. Duplicate relative humidity daily minima were compared with t-tests (alpha = 0.05).

Since low humidity is considered a problem for some riparian dependant flora and fauna, data analysis focused on daily minima and number of hours per day relative humidity was less than 50%. For each day the lowest relative humidity reading observed for each transect point was used. Daily minima for each row (3 replicates) were pooled and compared to successive distances from the stream. The same procedures were conducted with the daily length of time (hrs) relative humidity was less than 50%. The 50% point was arbitrarily selected after reviewing the 1996 pilot

data, because in dry conditions the value was typically between daily maxima and minima and changes in relative humidity occurred rapidly through that value.

Mean minimum relative humidity (mmRH) and mean length of time less than 50% relative humidity were compared at successive distances from the stream with analysis of variance (ANOVA). An ANOVA first tested if there were differences across the 30 m transect. Four a priori orthogonal contrasts were employed to evaluate successive distances from stream edge: 0 m vs. 5 m, 5 m vs. 10 m, 10 m vs. 20 m and 20 m vs. 30 m. Each daily RH minimum and length of time < 50% was an observation. Sample size (number of days) for the Teanaway sites was seven, Klickitat was nine, and Grande Ronde was five with each day treated as a replicate observation. Multiple linear regression was employed to determine if the site characteristics (percent shade and basal area) could explain the differences in mmRH within each site.

Results

The 12 eastside locations were located within three watersheds: Teanaway River, Klickitat River, and Grande Ronde River watersheds (Figure 1). Site characteristics of these second to third order streams are presented in Table 1. Stream gradients ranged from 2 to 9 percent with widths at the time of measurement ranging from 1.3 to 5 m. Percentage of tree diameter size distribution at each site varied with 10-20 cm dbh and 20-40 cm dbh size categories predominant at all sites (Table 1). Understory vegetation was highly variable (Table 2). Shrubs were usually the dominant understory, but no trend with distance from stream was observed. Within the sites of the three watersheds the tree basal area and resultant shade varied, with the Teanaway watershed having the lowest percent shade and basal area and Grande Ronde watershed with the most. There was no general trend with respect to shade and basal area at distance from the stream. In some cases it was highest at stream edge; while at others it could be at any transect point (Table 1).

During the period of the study the maximum air temperatures were 32°C in La Grande, 30°C in Ellensburg and 33°C in Goldendale. Maximum relative humidity levels were at or near 100% for

TABLE 1. Characteristics of twelve study sites located in three areas east of the Cascade Mountains in eastern Oregon and Washington.

Watershed/Stream	Sample Dates	Grade (%)	Width (m)	Aspect (°)	Elevation (m)	Proportion of stems (%) by DBH Class (cm) 0-10	10-20	20-40	>40	Shade (%) by distance from stream edge (m) 0	5	10	20	30	Control	Basal Area (ft²/ac) by distance from stream (m) 0	5	10	20	30
Teanaway	7/17-7/25																			
Jack Creek		2	3.9	350	796	0	80	19	1	78	92	64	32	26	3	20	20	20	20	20
Middle Creek		4	1.8	190	753	0	90	2	8	6	7	2	22	100	0	3	3	0	0	50
Wilson Creek		9	4.2	228	978	0	60	20	20	27	38	78	93	22	0	3	20	40	70	50
Cooke Creek		3	5.0	280	893	0	10	80	10	39	62	53	74	6	7	40	60	60	50	70
Klickitat	7/27-8/5																			
Dry Creek trib.		6	1.4	66	911	0	60	35	5	95	90	98	40	6	17	80	50	60	10	20
Highland Canyon (rb)		2	1.5	79	881	0	30	50	20	78	91	82	70	11	15	70	100	120	70	40
Highland Canyon (lb)		2	1.5	259	881	0	20	50	30	49	78	60	65	67	1	60	70	80	80	90
West Prong Creek		4	4.0	56	729	0	20	40	40	58	95	72	27	44	3	70	50	50	80	100
Grande Ronde	8/8-8/12																			
Grossman Creek		3	2.0	340	1151	10	20	50	20	78	80	65	40	100	0	45	60	70	80	100
Gordon Creek		3	2.8	70	972	0	25	50	25	83	75	85	50	20	0	150	130	100	70	90
Indian Creek		3	1.3	70	1185	10	25	40	25	25	80	79	85	80	0	80	140	130	160	150
Little Catherine Creek		3.5	5.0	300	1094	10	25	50	15	28	53	82	80	85	0	30	100	150	200	220

TABLE 2. Volume occupance (%) of grasses (G), shrubs (S), and tree branches (T) in a 1 m x 0.5 m cylinder at transect points in streams of three watersheds. Distances values 0, 5, and 10 m are means of 3 replicates (C is control.)

Watershed/Stream	Volume Occupance (%)											
Distance (m)	G	S	T	G	S	T	G	S	T	G	S	T
Teanaway		Jack			Middle			Wilson			Cooke	
0	0	2	10	1	0	0	2	26	0	0	0	0
5	1	15	37	62	12	0	1	2	1	2	3	0
10	10	19	23	43	29	0	0	3	2	2	2	0
20	5	0	0	5	0	10	0	1	0	10	0	0
30	0	15	0	0	2	5	0	2	0	0	5	0
C	0	0	0	1	20	0	2	0	0	2	0	0
Klickitat		Dry			Highland (rb)			Highland (lb)			West Prong	
0	0	1	3	2	4	5	0	75	0	0	1	0
5	0	43	10	2	2	13	3	2	0.3	0.3	1	0
10	0	9	3	1	1	0	0	29	0	0	3	0
20	5	0	0	3	2	0	2	0	0	0	2	0
30	1	2	0	1	2	0	1	0	0	1	15	0
C	0	20	0	10	0	0	5	0	0	0	0	0
Grande Ronde		Grossman			Gordon			Indian			Little Catherine	
0	8	13	0	0	3	0	25	16	0	0	5	0
5	13	29	3	3	33.3	0	3	5	0	7	15	5
10	0	25	5	2	12	3	0	8	0	3	16	3
20	10	40	10	10	50	0	10	0	10	0	10	0
30	0	10	0	10	30	0	0	10	0	0	15	0
C	5	10	0	10	60	0	10	30	0	5	0	0

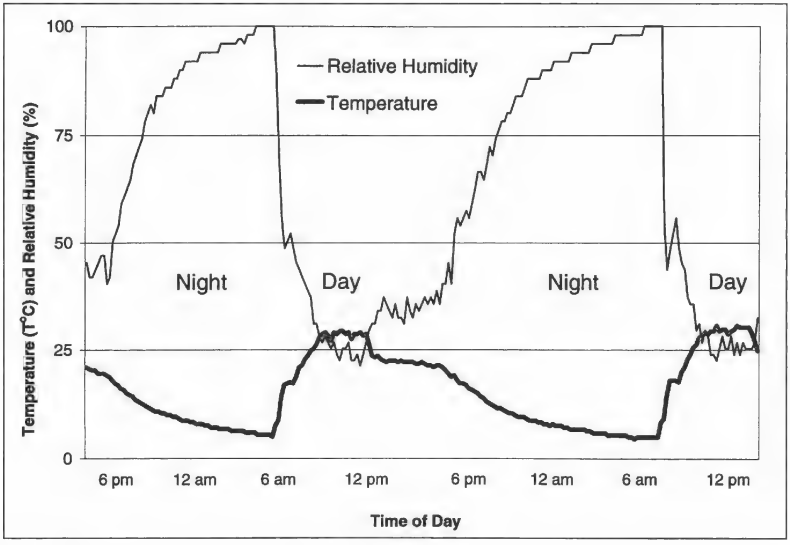

Figure 3. Example of diurnal pattern of temperature and relative humidity observed at all sites during the study.

all sites at all transect points. These values were reached nightly and remained near 100% until after sunrise, sharply declining as air temperature rose (Figure 3). Quality assurance tests after the study found all but one of the relative humidity instruments to meet the standard, with duplicate precision of daily mmRH was greater than 98% for the instruments.

At all sites there were significant differences (P value < 0.05) in mean minimum relative humidity (mmRH) across the 30 m transect except for one, Grossman Creek (Table 3). In the successive contrasts 9 of 12 had significant differences in mmRH between stream edge and 5 m. Two of the remaining three had a significant difference between 5 to 10 m from the stream edge. Between transect points 10 m from the stream and beyond there were few additional changes in mmRH, only two for each the 10–20 m and 20–30 m comparisons (Table 3). Figure 4 illustrates the general decreasing trend of mmRH with distance from the stream edge. The figure includes the control site, which was in an opening with minimal shade and farther from the stream than the 30 m transect points. At only the Klickitat sites did all 4 sites during a sampling interval respond similarly (Figure 4), suggesting that even with similar climate, local topography can influence gradient structure.

Results of the comparison of mean length of time less than 50% relative humidity had largely identical results (Table 4). In general, distance from the stream and the length of time RH was less than 50% were positively correlated. Overall the length of time of RH < 50% stabilized 5 to 10 m from stream edge (Figure 4; Table 4).

At one stream, Highland Canyon Creek, transects were deployed on both sides of the stream. Results of mmRH and length of time less than 50% RH were very similar on each side with one exception. Between 10–20 m on the left bank there was no difference in length of time less than 50% (Table 4). This is likely a result of a topographic feature, as there is negative slope between those two transect points (Table 5).

The effect of local topography on the RH gradient can be seen in many of the sites. Middle and Wilson Creeks have the least topographic slope (Table 5) and only minor changes (+ and -) in mmRH. At the Grande Ronde sites, the site with the highest near stream slope, Gordon Creek, had the most pronounced change in mmRH and time <50% between 0 and 5 m (Tables 3 and 4; Figure 4). The same pattern was observed at the Klickitat sites, Dry and Highland Canyon Creeks. Vegetation density and structure did not exert as strong an influence as local topography. Mean minimum relative humidity was regressed against percent shade and basal area and had coefficients of determination (r^2) ranging from 0.09 (West Prong Creek) to 0.80 (Little Catherine) (Table 6). Only four site regressions were significant (P< 0.05). Overall differences in microclimate conditions across the gradient followed no pattern with the exception of higher daytime relative humidities very close to the stream.

Discussion

These study sites were located in a variety of locations with different site conditions across the eastside of the Cascade Mountains in Washington and Oregon. While there are certainly other conditions represented east of the Cascades that may exhibit different moisture gradient conditions (such as in larger streams and rivers or within a

TABLE 3. Analysis of variance (ANOVA) probability values of mean minimum relative humidity (mmRH) across 30 m transect and orthogonal contrasts between adjacent transect points for mmRH at twelve sites in eastern Oregon and Washington.

			Orthogonal Contrasts (P-values)			
Watershed	Stream	ANOVA	0-5 m	5-10 m	10-20 m	20-30 m
Teanaway	Jack Creek	< 0.001	<0.001	<0.001	0.041	0.281
	Middle Creek	0.0001	0.734	0.013	0.395	0.867
	Wilson Creek	0.0001	<0.001	0.016	0.688	0.055
	Cooke Creek	0.0069	0.056	0.140	0.342	0.130
Klickitat	Dry Creek trib.	< 0.001	<0.001	0.036	0.028	0.418
	Highland Canyon (rb)	< 0.001	<0.001	1	0.275	0.466
	Highland Canyon (lb)	< 0.001	<0.001	0.803	0.177	0.930
	West Prong Creek	< 0.001	<0.001	0.314	0.372	0.778
Grande Ronde	Grossman Creek	0.0568	0.947	0.028	0.882	0.772
	Gordon Creek	< 0.001	<0.001	0.007	0.417	0.007
	Indian Creek	< 0.001	0.047	0.074	0.067	0.013
	Little Catherine Creek	< 0.001	<0.001	0.260	0.525	0.820

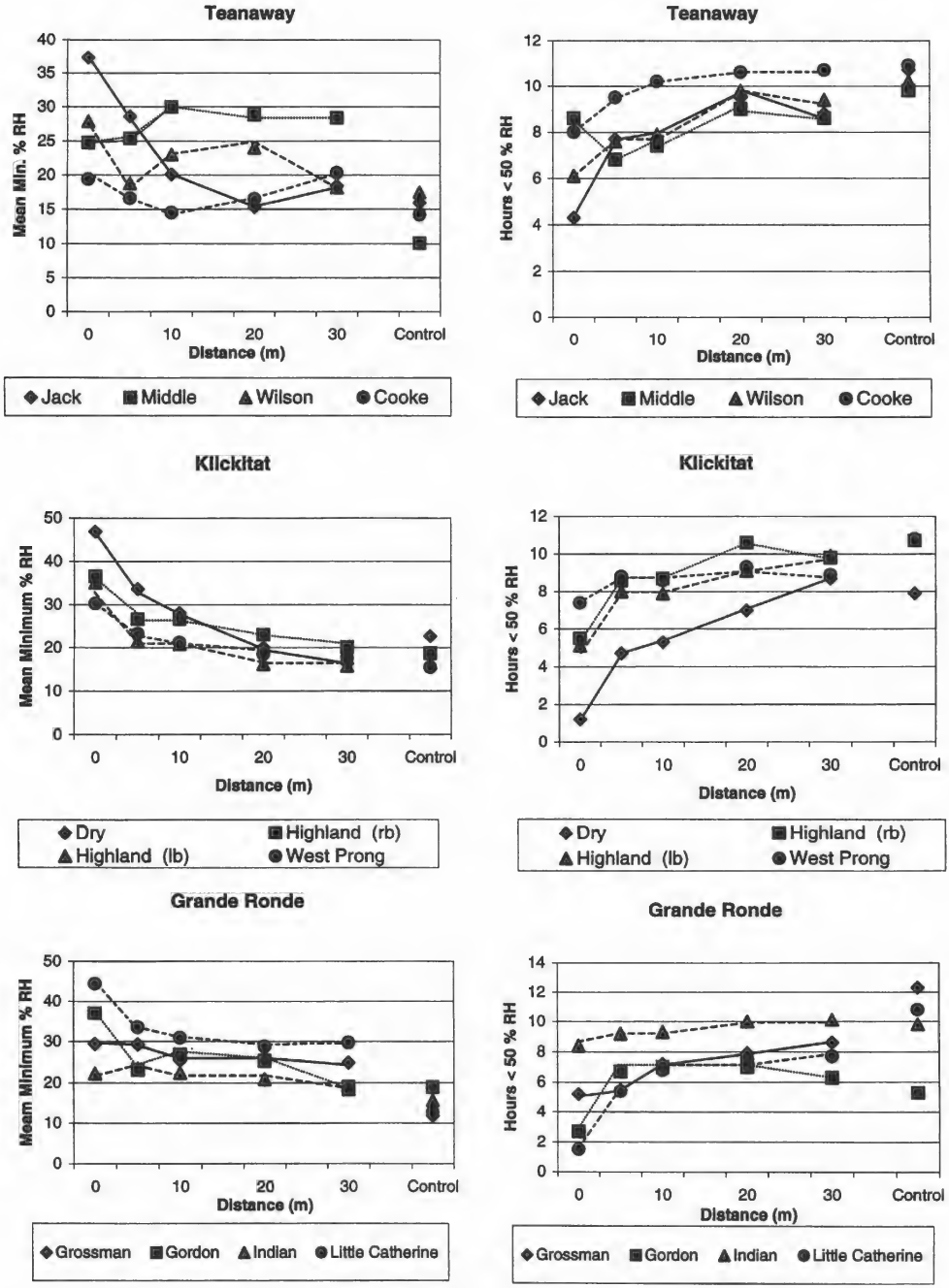

Figure 4. Mean minimum relative humidity (mmRH) and % time < 50 % RH in four stream riparian areas for each of three locations.

TABLE 4. Analysis of variance (ANOVA) probability values of length of time relative humidity (RH) < 50% across 30 m transect and orthogonal contrasts between adjacent transect points for length of time (hrs.) < 50% RH at twelve sites in eastern Oregon and Washington.

Watershed	Stream	ANOVA	Orthogonal Contrasts (*P*-values) 0-5 m	5-10 m	10-20 m	20-30 m
Teanaway	Jack Creek	<0.001	<0.001	0.914	0.004	0.347
	Middle Creek	0.0026	0.0011	0.326	0.033	0.679
	Wilson Creek	<0.001	0.001	0.372	<0.001	0.547
	Cooke Creek	<0.001	<0.001	0.015	0.333	0.722
Klickitat	Dry Creek trib.	<0.001	<0.001	0.141	0.008	0.016
	Highland Canyon (rb)	<0.001	<0.001	0.791	0.012	0.419
	Highland Canyon (lb)	<0.001	<0.001	0.858	0.033	0.252
	West Prong Creek	0.011	0.005	0.675	0.215	0.536
Grand Ronde	Grossman Creek	<0.001	0.564	0.002	0.415	0.453
	Gordon Creek	<0.001	<0.001	0.307	0.947	0.440
	Indian Creek	<0.001	<0.001	0.754	<0.001	0.661
	Little Catherine Creek	<0.001	<0.001	0.073	0.485	0.938

TABLE 5. Topographic slope between successive transect points (Distances 0, 5, and 10 m values are means of 3 replicates.).

Stream	Distance Interval (m) 0-5	5-10	10-20	20-30
Jack Creek	10	9	12	20
Middle Creek	9	2	6	8
Wilson Creek	7	7	4	4
Cooke Creek	31	23	4	17
Dry Creek trib.	29	12	3	64
Highland Canyon (rb)	51	67	16	46
Highland Canyon (lb)	21	-6	11	41
West Prong Creek	14	3	1	-3
Grossman Creek	7	40	33	30
Gordon Creek	32	2	5	7
Indian Creek	15	9	30	52
Little Catherine Creek	13	13	48	30

TABLE 6. Coefficients of determination and probability values for regressions at each site of mean minimum relative humidity with percent shade and basal area as the independent variables.

Location	r^2	*P*-value
Teanaway Watershed		
Jack Creek	0.65	0.015
Middle Creek	0.52	0.055
Wilson Creek	0.17	0.46
Cooke Creek	0.13	0.66
Klickitat Watershed		
Dry Creek trib.	0.66	0.012
Highland Canyon (rb)	0.16	0.48
Highland Canyon (lb)	0.55	0.04
West Prong Creek	0.09	0.67
Grande Ronde Watershed		
Grossman Creek	0.23	0.35
Gordon Creek	0.3	0.23
Indian Creek	0.26	0.3
Little Catherine Creek	0.8	0.0015

different range of elevation), these sites do represent major areas of eastside forests. Moderately open stands are common within the forested stands of these areas (Quigley et al. 1997). The actual edge of the regulated buffer and the managed stand also varies, although the edge between the regulated buffer and the existing stand in all cases of these study sites occurred within the 30 m study width. The percent shade and basal area of the 30 m transect point was representative of the adjacent forest with shade ranging from 6–100% and basal area 20 to 220 ft^2/ac; however, given the silvicultural prescription of selective harvest, the canopy cover was not uniform. The inability of shade and basal area to explain the relative humidity gradient in the regression analyses at these sites is likely due to the high variability in shade and basal area in these forest types both in the unmanaged riparian buffer and the upland stand.

These site conditions were very different from the westside study sites that have been used to assist in the understanding of microclimate gradients in riparian ecosystems in the west. The original study of microclimate gradients in the

Pacific Northwest by Chen et al. (1995) compared the distance from clear-cut edges into a mature forest. That approach is different from this study which is from a stream edge out into an adjoining forest. This study considers additional factors that can influence local climate such as valley structure and the stream as a water source that were not included in the Chen et al. study. Topographic and stream factors likely contribute to the steep gradients observed in this study. The lack of change in relative humidity seen after usually 10 m in this study, was a shorter distance than observed by Brosofske et al. (1997). Using an approach similar to the one employed in this study, Brosofske found little change in relative humidity after 31 m in western Washington riparian areas. This difference between eastern and western Cascade sites is likely due to climatic (cooler with more precipitation) and biological factors such as a denser and more uniform forest.

The extreme dry condition of low elevation forests of eastern Washington and Oregon creates an arid environment that aids in maintaining a naturally low tree density, with openings common, and sets the stage for a much more frequent fire regime (Agee 1993). With the Cascade Mountains intercepting moisture carried in air masses moving east, the summer air is dry. Therefore riparian zones are the critical habitat areas for a wide array of organisms. The results of this study found that area to be very narrow.

The sources of moisture in these dry habitats will be the remaining soil moisture, moisture carried by the atmosphere, any transpiration, and the stream itself. While the atmosphere may occasionally bring precipitation, the available soil moisture will be steadily decreasing as the summer progresses. During spring and early summer, evaporation from the soil and transpiration from the surrounding forest are likely major contributors to local air moisture content (Spurr and Barnes 1973). Growth and associated transpiration slows steadily as summer continues, with little to any new growth occurring during mid to late summer (Oliver and Ryker 1990). One response of plants to periods of water stress is the partial or full closing leaf stomata, limiting water losses to the atmosphere (Kozlowski et al. 1991). The remaining sources of air moisture are either direct, through stream evaporation, or indirect, through the limited transpiration of riparian vegetation immediately adjacent to the channel. This limits the amount of moisture available, such that only narrow bands of unique microclimate can be supported.

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Water Table Dynamics and Soil Texture of Three Riparian Plant Communities

Abstract

Restoration of degraded riparian plant communities must consider relationships among water table dynamics, soil texture, and plant species. We compared water table dynamics, soil texture, and slope among riparian plant communities dominated by: 1) beaked sedge (*Carex rostrata* Stokes), 2) Geyer's willow (*Salix geyeriana* Anderss.), and 3) black cottonwood (*Populus trichocarpa* T. & G. ex Hook) occurring on recent alluvial bars. We examined six sites of each plant community in western Montana. Mean bimonthly fluctuation in water table depth did not differ among the three plant communities (P = 0.67), but mean depth to water table was greatest (P = 0.004) in the cottonwood community (62.8 cm), intermediate for the willow (32.0 cm) and least for sedge communities (20.7 cm). Soil texture differed among the three plant communities for sand (P =0.0004), silt (P = 0.0002), and clay (P = 0.003). Cottonwood communities occurred on soils that averaged 78% sand, whereas sedge and willow sites averaged 47% sand and 35% sand, respectively. Silt content was 40% beneath willow, 35% beneath sedge and 15% beneath cottonwood communities. Soils of the willow sites averaged 25% clay compared with 18% and 7% for sedge and cottonwood communities, respectively. Soils beneath all three plant communities differed in coarse fragment percentage (P = 0.01), averaging 46% in cottonwood, 22% in willow, and 15% in sedge sites. We found no differences in slope among the three plant communities, either parallel to the stream (P = 0.76) or perpendicular to the stream (P = 0.29). Thus, these plant species exhibit a more narrow affinity for soil texture, coarse fragment content and water table depth than previously reported.

Introduction

Riparian ecosystems tend to be very dynamic changing dramatically through time and space (Padgett et al. 1989). Frequent and dramatic changes occur because of the constant reworking of stream substrates, the presence of side channels, topographic variability and regular flooding. In the wake of these abiotic interactions, managers need to know how changes in water flow (Fenner et al. 1985) influence riparian vegetation and how soil texture relates to both riparian vegetation (Hansen et al. 1995) and the water table (Friedman et al. 1997).

As a first attempt, to better understand riparian ecosystems several riparian vegetation classification systems have been developed to aid land managers in the western United States. These include classifications for eastern Idaho-western Wyoming (Youngblood et al. 1985), southern Oregon (Kovalchik 1987), Utah and southeastern Idaho (Padgett et al. 1989), Nevada and eastern California (Manning and Padgett 1995) and Montana (Hansen et al. 1995). All of these publications contain valuable information about successional pathways, soil pedon descriptions, and land management recommendations, but they typically contain only broad, casual observations of soil texture and water tables, even though these variables greatly influence the distribution of plant communities (Brady 1990). According to Hansen et al. (1995), soils are generally thought to influence riparian species composition, species coverage, and growth form. Groundwater may affect

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riparian vegetation more than soil characteristics (Hansen et al. 1995) and effects of water table declines are related to soil textures (Friedman et al. 1997). Therefore, increased understanding about the influence of soil texture and water table dynamics may improve efforts to identify the successional status of riparian communities and aid in the restoration of degraded riparian areas. The purpose of our study was to further define the ecological range of three riparian communities that are ubiquitous throughout the northern Rocky Mountains (Hansen et al. 1988).

Study Areas

We compared water table dynamics, soil texture, and slope among riparian plant communities dominated by: 1) beaked sedge (*Carex rostrata* Stokes), 2) Geyer's willow (*Salix geyeriana* Anderss.), and 3) black cottonwood (*Populus trichocarpa* T. & G. ex Hook) occurring on recent alluvial bars. Sites were classified according to Hansen et al. (1995). For each of the three plant communities, we examined six representative sites in western Montana. Study sites were located across a broad range of mountain valley landscapes at elevations from 1000 to 1460 m (Figure 1). Average annual precipitation across all sites ranged from 584.2 – 711.2 mm with most of the precipitation occurring in May and June. Average annual air temperature across all sites was 3°C.

Cottonwood Sites

The black cottonwood recent alluvial bar communities are early seral communities that require freshly deposited alluvium as a seedbed (Hansen et al. 1995). Two sites were on sandy to cobbly alluvium on glacial outwash along the Blackfoot River in a narrow mountain valley near Ovando, Montana. The remaining four sites were adjacent to the Gallatin River, which drains the wide Gallatin Valley, near Bozeman and Three Forks, Montana. Alluvial fill at these sites was a mixture of cobbles and boulders.

Sedge Sites

Two sites were adjacent to Railroad Creek (meandering meadow stream) near Norris, Montana. Railroad Creek occupies a broad valley floor and drains finely sorted gravel/cobble alluvium.

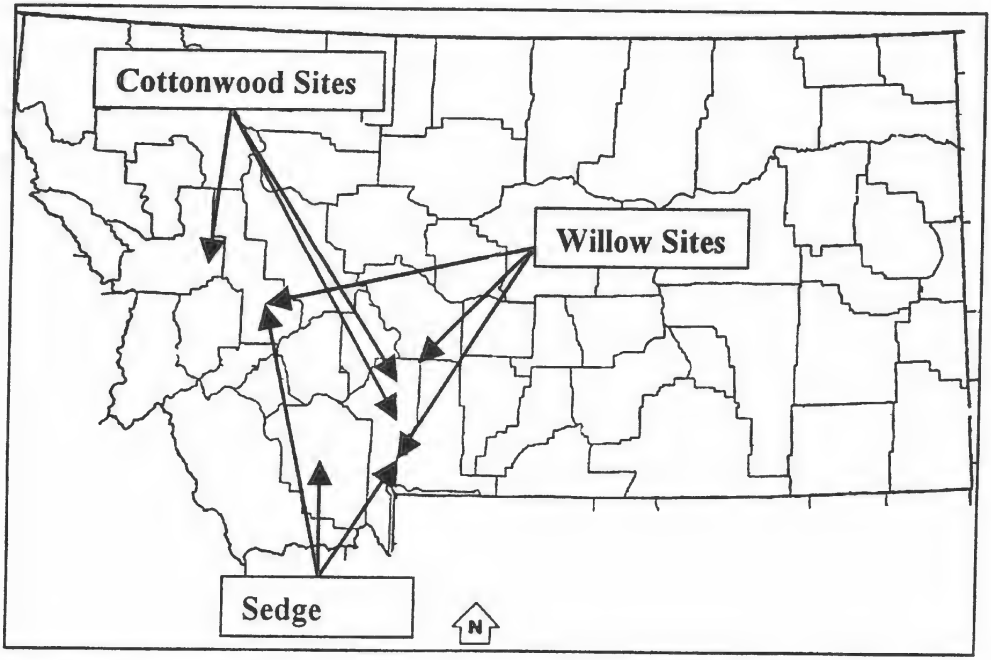

Figure 1. Map of Montana. Each arrow represents two sampling locations for each community type.

Archean granite is the primary parent material. Two other sedge sites were adjacent to Shanley and Lynn Creeks (meandering meadow streams) near Ovando, Montana. These two streams drain a rolling landform of glacial outwash and lateral moraines. Soils contain mixtures of sand, pebbles, gravel, cobbles, and boulders. The remaining two sedge sites were adjacent to Hyalite Creek (mountain stream) south of Bozeman, Montana. Tertiary volcanics and Madison limestone compose the alluvial parent material. Cobbles and gravel dominate the soil mix.

Willow Sites

Two sites were near Ovando, Montana along Cottonwood Creek (meandering meadow stream). This stream drained a rolling landform of glacial outwash and lateral moraines. Soils contained mixtures of sand, pebbles, gravel, cobbles, and boulders. Two other willow sites were along Brackett Creek (mountain stream) northeast of Bozeman, Montana. The stream was formed over silt and mudstones from Jurassic-aged formations. The remaining two willow sites were adjacent to Hyalite Creek (mountain stream) south of Bozeman, Montana. Soils were derived from Tertiary volcanics and Madison limestone.

Methods

A 10 × 10 m macroplot was established at each of the 18 sites. Botanical composition was sampled to verify that site classification followed Hansen et al. (1995). Vegetative canopy cover, by species and by life form, was sampled via the Canopy Coverage Method along two 10 m transects located near the center of each macroplot (Daubenmire 1959). Estimates of herbaceous canopy cover were obtained from 25 × 50 cm quadrats placed along each transect at 1 m intervals.

Water And Soil Sampling

Water table depth was measured to the nearest centimeter in three shallow wells located near the center of each macroplot. Each well was constructed of 1.9 cm × 1.5 m schedule 40 perforated steel pipe placed into the soil to a depth of 1 m. Wells were spaced at 3 m intervals along an upslope gradient perpendicular from the stream. Depth to water table and water table fluctuation was measured bimonthly from June through October in 1997 and 1998. Water table fluctuation was calculated by subtracting each two-week measurement from the one previous.

Soil samples were collected from three 51 cm deep pits on each site. Pits were located 1 m away from the water wells. Due to the lack of horizonation in each pit, we chose to subsample each pit at four arbitrary depths (0-13, 14-25, 26-38 and 39-51 cm). The texture of each of the four strata was averaged to represent the whole soil pit. Prior to analyzing the samples for texture, coarse fragments were separated from each soil sample. A 2 mm sieve was used to separate larger fragments from the soil that were then weighed to determine their percentage of the total soil weight. Soil texture was analyzed using the hydrometer method (Bouyoucos 1936, Day 1965, Gee and Bauder 1979) on each of the four subsamples.

Slope of each macroplot was measured perpendicular to the stream and parallel to the stream. A stadia rod and abney level were used to measure slope over a distance of 6 m.

Statistical Analyses

Water table depth and fluctuation were compared among plant communities using a three-stage repeated measures ANOVA. Prior to the ANOVA, a square-root transformation was applied to the water table fluctuation data to achieve normality. A three-stage nested ANOVA was used to compare particle size (soil texture) and coarse fragment percentages among the three plant communities, and slope was compared using a nested ANOVA. A square-root transformation was also applied to the coarse fragment and slope data to achieve normality prior to ANOVA testing. All differences were declared significant at $P \leq 0.10$. Mean separation was accomplished with Bonferroni multiple comparison tests (Neter et al. 1996).

Results

Bimonthly mean water table fluctuation (Table 1, Figure 2) averaged 7.0 cm and did not differ among the three plant communities ($P = 0.67$). Mean depth to water table (Table 1, Figure 3) significantly differed between the three communities and was greatest ($P = 0.004$) for the cottonwood communities (63 cm). The willow depth (32 cm) to the water table was intermediate and

TABLE 1. Mean (± SE) two-year growing season values for several site variables of black cottonwood recent alluvial bar, Geyer's willow and beaked sedge riparian plant communities in western Montana.

Site Variable	Plant Community Type[1]		
	Cottonwood	Willow	Sedge
Water Table			
Water Table Depth (cm)	63 ± 2.7[a]	32 ± 2.3[b]	21 ± 1.1[c]
Water Table Fluctuation (cm)	11 ± 0.4[a]	5 ± 0.2[a]	5 ± 0.1[a]
Soil Texture			
%Sand	78 ± 2.3[a]	35 ± 2.2[b]	47 ± 2.7[c]
%Silt	15 ± 1.8[a]	40 ± 1.2[b]	35 ± 1.8[c]
%Clay	7 ± 0.6[a]	25 ± 1.5[b]	18 ± 1.2[c]
%Coarse Fragments	46 ± 1.1[a]	22 ± 0.5[b]	15 ± 0.3[c]
Slope			
Parallel Slope (°)	0.6 ± 0.02[a]	1.0 ± 0.1[a]	1.0 ± 0.2[a]
Perpendicular Slope (°)	0.6 ± 0.1[a]	1.6 ± 0.2[a]	0.8 ± 0.02[a]

[1]Means within rows followed by the same lowercase letter are not different ($p > 0.10$) using Bonferroni multiple comparison tests (Neter et al. 1996).

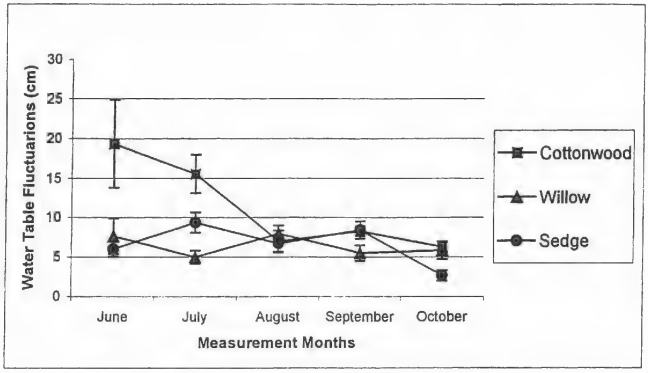

Figure 2. Mean 1997-1998 monthly water table fluctuations for each community type; error bars represent the standard error ($\sigma/\sqrt{n}$) of the sampling distribution (Ott and Mendenhall 1994).

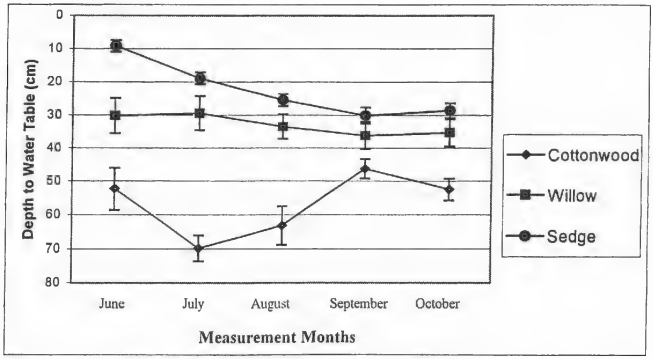

Figure 3. Mean 1997-1998 monthly depth to water table values for each community type; error bars represent the standard error ($\sigma/\sqrt{n}$) of the sampling distribution (Ott and Mendenhall 1994).

the sedge depth (21 cm) to water table was the shallowest.

Soil texture differed among the three plant communities (Table 1) for sand ($P = 0.0004$), silt ($P = 0.0002$), and clay ($P = 0.003$). Cottonwood soils were sandier (78% sand) than sedge soils, which were sandier (47% sand) than willow (35% sand) soils. Cottonwood soils also contained less clay (7% clay) and silt (15% silt) than sedge soils, which contained less clay (18% clay) and silt (35% silt) than willow soils which contained 25% clay and 40% silt. Sampled coarse fragments measured 2.1 mm to 11 cm and mean coarse fragment percentages differed among the three community types ($P = 0.01$). Cottonwood soils contained the most coarse fragment percentages (46%), willow soils were intermediate (22%) and sedge soils contained the least (15%).

We found no differences in slope among the three plant communities (Table 1), either parallel to the stream ($P = 0.76$) or perpendicular to the stream ($P = 0.29$). Across all sites, parallel slopes averaged 0.9° (1%) and perpendicular slopes averaged 1.0° (1%).

While the three riparian communities covered in this study experienced similar water table fluctuations of 0–0.11 m and occupied gradients of 0.67–1.0%, there were significant differences in soil texture, percent of coarse fragments and depth to water table. These differences indicate that black cottonwood recent alluvial bar, Geyer's willow and beaked sedge communities occupy specific sites within the riparian zone.

Black cottonwoods occurring on recent alluvial bars occupy gravelly loamy sand soils (46% coarse fragments). Groundwater within these communities has a mean depth of 0.6 m. Mean depth to water table is 0.3 m in Geyer's willow communities and they occur on sites with gravelly loam soils (22% coarse fragments). Beaked sedge communities grow on sites with loam soils (15% coarse fragments) and a mean depth to water of 0.2 m.

Discussion

While there are a number of publications describing the physical characteristics of certain riparian communities, few of the descriptions provide enough detail to be of use to a resource manager when evaluating revegetation potential on a degraded riparian site. Not only are the descriptions too general but they offer contradictory information. For example, Kauffman et al. (1985) found cottonwood soils, along Catherine Creek in northeastern Oregon, to be well-drained loamy soils with sand, gravel and cobbles while a similar community type in Montana was described as occurring on silt loam soils (Hansen et al. 1995). Manning and Padgett (1995) reported that beaked sedge communities occurred on clayey sites while Hansen (1995) described soils under beaked sedge communities as loamy clay to sandy loam. The only area of general agreement appears to be the soil textural class for Geyer's willow communities.

Youngblood et al. (1985), Manning and Padgett (1995) and Hansen et al. (1995) reported that Geyer's willow communities occupied fine textured soils (clayey and fine-loamy textures). However, this description suggests substantial overlap with the beaked sedge community type (clayey to sandy loam). Based on the successional models for Rocky Mountain montane and subalpine wetlands described by Windell et al. (1986) changes in soil textural classes should be reflected by differences in riparian community composition. Thus, the presence of a particular soil texture should dictate the occurrence of a particular riparian community, e.g., Geyer's willow or beaked sedge. However, Manning and Padgett (1995) and Hansen et al. (1995) report the same soil textural class for both beaked sedge communities and Geyer's willow communities. This poses a question for the resource manager trying to rehabilitate a degraded riparian area; revegetate with sedge or willow? Judgements about which species to use becomes even more complex if the Hansen et al. (1995) description of cottonwood soils is included in the decision making process; sedges, willows and cottonwoods all appear to occur on fine-loamy textured soils. The question then arises as to whether or not the depth to water table is equally variable.

Stream loss, snowmelt, and precipitation infiltration recharge groundwater lost through wells, springs, and evapotranspiration. The interaction between drawdown and recharge rates can cause considerable daily and seasonal water table fluctuation (Hackett et al. 1960). One might assume that, given different soil textures, coarse fragment percentages, and depth to water table that water table fluctuation would also be significantly different among the community types, yet they were

not. Although there is some temporal variability (Figure 2), especially in the cottonwood communities, this parameter, alone, does not separate the three community types. This may be due to the fact that spring runoff and precipitation events are very similar across the sites. Also, the water table at some cottonwood sites began to drop below 1 m from the soil surface in late July. Fluctuations below 1 m were not taken into account. Thus, the temporal variability in water table fluctuations of the cottonwood sites could not be included in the analysis when this occurred (Table 2).

TABLE 2. High and low water table depths and fluctuations during the growing season across the cottonwood recent alluvial bar, Geyer's willow and beaked sedge riparian plant communities in western Montana.

Site Variable		Plant Community Type Cottonwood	Willow	Sedge
Water Table				
Water Table Depth (cm)	High	>100.0	>100.0	48.0
	Low	4.0	0.0	0.0
Water Table Fluctuation (cm)[1]	High	49.0	59.0	30.0
	Low	1.0	0.0	0.0

[1]Some cottonwood sites and one willow site's water table fluctuations occurred below 1 m at the later part of the growing seasons and were not included.

Water table depth and soil texture partially regulate soil Eh (aeration) and water availability, and both influence the potential of a site to support a given plant community (Brady 1990). Because oxygen is essential for root growth in all plant species (Yamasaki 1952), woody species are particularly dependent on well-watered and well-drained substrates (Pezeshki et al. 1998). It follows that Pezeshki et al. (1998) found net carbon fixation of black willow (*Salix nigra*) to be highest in well-watered and well-drained conditions. Also, total black willow root biomass, at a variety of soil depths, decreased significantly under low soil aeration. Black willow posts (cuttings) exposed to continuously flooded conditions next to creeks experienced 80% mortality, and 79% of live root biomass was within 15 cm of the soil surface in continuously flooded conditions. Baldcypress (*Taxodium distichum*) and oaks (*Quercus* spp.) also exhibit this trend (Pezeshki 1991). Ewing (1996) showed that 2-year-old saplings of Oregon ash (*Fraxinus latifolia*) and red alder (*Alnus rubra*) died in static flooding to or above the soil surface and experienced decreased photosynthesis and growth in cycles of flooding and drying.

Anaerobic microbial respiration (Mitsch and Gosselink 1993) and chemical reactions such as the production of soluble iron, manganese, ethanol, acetaldehyde, and cyanogenic compounds and pH changes (Kozlowski, 1984) in continuously flooded soils may cause nutrients to become unavailable or toxic to plants. Root respiration also is constrained under reduced conditions, which limits the supply of energy to the roots and reduces their ability to absorb nutrients (Brady 1990). These relationships may explain why both cottonwoods and willows occupy sandy and gravelly sites where water tables remain relatively low.

Unlike woody species, beaked sedge apparently tolerates root zone saturation (Ewing 1996). High water tables influence beaked sedge distribution more than soil substrate properties (Youngblood et al. 1985). In support of this observation, Manning and Padgett (1995) stated that beaked sedge colonizes permanently flooded sites. Kauffman et al. (1985) described sedge soils, in northeastern Oregon, as having fine-textured A-horizons above coarse-textured horizons that discouraged percolation. Even though the sedge and willow communities covered by this study occurred on loam soils, there were more coarse fragments in the willow communities (22%) than in the sedge-dominated communities (15%). The higher percentage of coarse fragments in the willow sites may allow the soil to drain quickly thereby quickly restoring soil oxygen levels following flooding. Differences in water table depth, 32 cm for willows and 21 cm for sedges, may explain why sedge communities convert to willow communities when a drop in the water table occurs (Hansen et al. 1988).

Conclusions

Results from our study can be used to reduce the apparent confusion over ecological site differences between these commonly occurring riparian communities and, thereby, improve the likelihood of riparian revegetation efforts. First, Geyer's willow communities occupy more coarse textured soils than beaked sedge communities (gravelly loams vs. loams) and contain more coarse fragments than the herbaceous type (22% vs. 15%).

Sites occupied by young cottonwoods will have the coarsest textured soils of the group (gravelly loamy sands) and have the highest percentage of coarse fragments (46%). Second, our results also indicate that further differentiation can be made between the three communities by measuring depth to the water table.

In the study beaked sedge communities occupied fine textured soils with 15% or less coarse fragments and a relatively shallow water table (0.2 m). This water table depth/plant community relationship is in agreement with the findings of Manning and Padgett (1995) and Youngblood et al. (1985). If depth to water table is 0.4 m or deeper and the soil is coarser (gravelly loam) and has a coarse fragment volume of at least 22%, Geyer's willows should dominate the site. Again, an earlier description of the Geyer's willow community (Hansen et al. 1995) reported the same depth to water table as we found in this study. Sites with gravelly loamy sandy soils and a mean water table depth of 0.6 m will most likely be occupied by young cottonwoods.

Based on these results we recommend that depth to water table, soil texture and percent of coarse fragments be included in riparian site inventories. As this information is gathered for other community types resource managers should be better able to identify potential natural communities that are realistic and to select plant communities that meet their management goals (Smith 1987).

Acknowledgements

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Northwest Science Notes

The purpose of "Notes" is to periodically publish short papers (typically less than five pages in length). There is no specific format or content required for articles published here, but all papers will be peer-reviewed and must be scientifically credible. Authors may contact the Editor about the suitability of manuscripts for this section.

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Chronological Dating of High-Elevation Dead and Dying Trees on Northern Vancouver Island, British Columbia

Abstract

We analyzed tree rings to determine the time of death for 18 moribund and dead trees used as roosts by bats on northern Vancouver Island. We crossdated 29 increment core samples with tree-ring chronologies of living trees to estimate when the trees died. After they die, yellow-cedar (*Chamaecyparis nootkatensis*) trees deteriorate slowly and remain standing for as long as 200 years. In contrast, few western hemlock (*Tsuga heterophylla*) and western white pine (*Pinus monticola*) snags persist longer than 100 years. The ages at which our sampled trees died were highly variable, with western white pine, western hemlock, and yellow-cedar exhibiting the narrowest to widest range of ages, respectively. Our findings highlight the long persistence of snags in high-elevation coastal forests and the centuries of ecological service that these trees provide to snag-dependent wildlife.

Introduction

Large moribund and dead trees are an important component of old-growth ecosystems in coastal forests of North America (Franklin and Spies 1991). These trees result from senescence, fire, disease, insect damage, or physical disturbance, and they provide critical habitat for many species of wildlife (Bunnell et al. 1999). Although high-elevation forests of British Columbia contain a relatively large proportion of snags (Lertzman and Krebs 1991), the ecosystem dynamics of these snags are poorly understood (Flanagan et al. 1998). High-elevation forests are under increasing pressure as timber harvesting extends into the subalpine, and managers must understand these forests better if they are to develop silvicultural systems capable of sustaining wildlife species that depend on dead and dying trees.

Information about snag dynamics in the Pacific Northwest is based primarily on low- and mid-elevation forests from Alaska (e.g., Hennon and Loopstra 1991) to Washington (e.g., Graham and Cromack 1982). One finding particularly relevant to management of snag-dependent wildlife is that snags decay slowly and can remain standing for as long as 276 years (Daniels et al. 1997). Little research has been done in high-elevation forests, where the trees are considerably smaller and the decay of snags is presumably slower (Flanagan et al. 1998).

The aim of the research described in this note was to undertake a dendrochronological examination of dead and dying trees found at high elevation in a coastal old-growth forest on northern Vancouver Island. We chose to restrict our sample to trees that were being used as roosts by

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bats (Family Vespertilionidae). Our intentions were to use crossdated tree rings to determine the year of tree death and to establish the number of years each tree has remained standing. These findings were placed in the context of an existing decay classification scheme.

Study Area

Our study was conducted on the upper slopes (700–1500 m asl) of Mt. Cain, northern Vancouver Island (50° 14' 00" N, 126° 19' 55" W; Figure 1). The area is transitional between the Coastal Western Hemlock and Mountain Hemlock biogeoclimatic zones (Klinka et al. 1991). Below 1100 m asl, forests are characterized by old-growth stands of uneven-aged western hemlock (*Tsuga heterophylla*), amabilis fir (*Abies amabilis*), western redcedar (*Thuja plicata*), coastal Douglas-fir (*Pseudotsuga menziesii*) and western white pine (*Pinus monticola*). Above 1100 m asl, forests at the site consist primarily of amabilis fir, yellow-cedar (*Chamaecyparis nootkatensis*) and mountain hemlock (*Tsuga mertensiana*) (Laroque and Smith 1999).

The climate of the Mt. Cain area is characterized as severe, with the growing season for trees limited to 2 months. Monthly air temperatures average 3° C and range from -5.1° C to 11.1° C. Total annual precipitation averages 2620 mm, with 69% falling as rain (Klinka et al. 1991). Although snowpack depths on April 1 can reach 6 m, the average snowpack depth is 3.75 m (British Columbia Snow Survey Station 3B01—Forbidden Plateau 1954–1998, 1130 m asl), with the soil often remaining unfrozen throughout the year (Klinka et al. 1991).

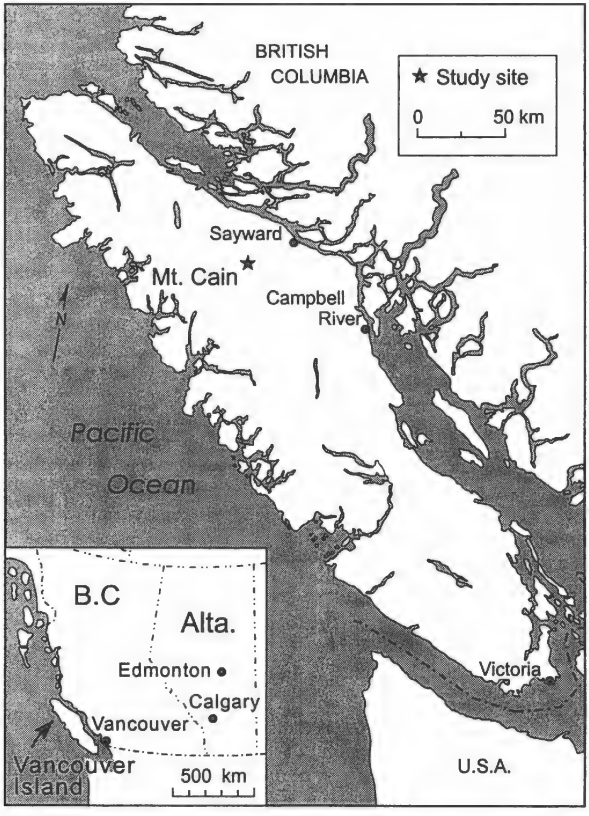

Figure 1. Location of the study site on Vancouver Island, British Columbia.

Methods

Eighteen dead or dying trees, at sites ranging from 700–1200 m asl, were used by bats as day roosts (Kellner 1999). We sampled all of these trees and, for each, we recorded tree species, diameter at breast height (dbh), height, and decay class (Guy and Manning 1994). We extracted 1–4 tree-ring samples at breast height from each tree using increment corers and standard dendrochronology methods (Fritts 1976). Chronologies were first visually crossdated using marker rings within each species group (Stokes and Smiley 1996). Following this analysis, a computerized measurement system (WinDENDRO™, Ver. 6.1) was used to measure individual ring-widths to the nearest 0.01 mm. Species-specific floating chronologies were developed for the 8 yellow-cedar, 8 western white pine and 13 western hemlock core samples.

Master living tree-ring chronologies were developed for western hemlock and yellow-cedar trees at the site (1000–1500 m asl). Sampling took place in 1994 and 1997, and involved the collection of increment cores from ca. 20 trees per species, with 2 radii sampled at breast-height on each tree. As with the dead and dying trees, ring widths were first visually cross-dated and then measured to the nearest 0.01 mm using the WinDENDRO™ system. Where ring boundaries were difficult to distinguish, a 40X microscope and Velmex-type stage measurement system were used for ring boundary verification. Measurement data were checked for crossdating errors by visually identifying common marker years (Stokes and Smiley 1996). Signal homogeneity was subsequently verified using the COFECHA computer program (Holmes et al. 1986). After crossdating, individual core measurements were standardized using the computer program ARSTAN (Holmes et al. 1986). A two-stage detrending method was used, in which the data were first detrended using a negative exponential curve or a linear trend and then were detrended a second time using a cubic-smoothing spline with a 50% frequency cutoff to remove any remaining inherent age/growth trends (Holmes et al. 1986).

Crossdating of the floating yellow-cedar and western hemlock chronologies established the growth period and year of death for the 4 yellow cedar and 8 western hemlock trees (Table 1). Some moribund trees were still producing an annual ring on radii during the year of sampling and so time of death for these samples was estimated at the year of sampling. We lacked a master chronology for western white pine and so could not crossdate 6 trees of this species. However, skeleton plotting confirmed that the western white pine samples had radial growth responses similar to that of western hemlock. Thus, we used the master chronology for western hemlock to estimate the year of death for the snags of western white pine (Table 1).

Results

The 18 trees used by roosting bats were either western hemlock, western white pine or yellow-cedar trees. They ranged in height from 15–49 m (mean 27 m) and in dbh from 40–108 cm (mean 65 cm) (1). Four of the 18 trees were in decay class 2 (live but unhealthy and dying trees), 10 were in decay class 4 (dead, no needles or twigs, 50% of the branches lost, loose bark, broken tops), and 4 were in decay class 5 (dead, most branches and bark absent, some decay). Ring counts indicated that the samples ranged in age from 106–562 years. Thirteen core samples still had bark attached. The other samples did not have bark, but the presence of bark elsewhere on each tree indicated that there was little loss of outer wood. However, we could not be certain that the outermost rings were always present in the sample, and therefore each sample is considered to be minimum-age dated.

Ring-width measurements from living western hemlock and yellow-cedar trees were used to develop two master chronologies. The western hemlock chronology spanned the interval from 1320–1997 AD (678 years) and the yellow-cedar series from 1205–1994 AD (790 years). The mean series correlations of both chronologies contained a collective signal significant at the 99% confidence interval when using 50-year chronology segments (values > 0.3281 significant). The yellow-cedar master chronology had a value of 0.45, and the western hemlock master series correlation was 0.34.

Discussion

Our dendrochronological assessment of snags at Mt. Cain shows that senescence in this environment follows a moribund period that varies from 50 years in the case of yellow-cedar to only 5–10 years in the case of western white pine. Although most trees died within the last century, some of these trees died between 1 and 2 centuries ago.

TABLE 1. Dendrochronological and morphological characteristics of 18 trees used as roosts by bats at Mt. Cain on northern Vancouver Island, British Columbia.

Tree species and identification name	Core number	Decay class	Dbh (cm)	Height (m)	Crossdated period	Length of section (years)	Year of tree death
Yellow-cedar (*Chamaecyparis nootkatensis)*							
1. Luther 3	3a	5	54	16.6	1164-1609	445	
	3b	5	54	16.6	1429-1689	260	
	3c	5	54	16.6	1222-1784	562	
	3d	5	54	16.6	1376-1789	413	1789
2. Joseph 2	2	2	87	20.6	1744-1996	252	1996
3. Her 1	1a	2	62	22.9	1671-1962	291	
	1b	2	62	22.9	1667-1987	320	1987
4. Her 2	2	4	78	19.8	1426-1950	524	1950
Western hemlock *(Tsuga heterophylla)*							
5. Luther 1	1a	5	55	15.3	1611-1991	380	1991
	1b	5	55	15.3	1617-1948	331	
6. Luther 2	2	5	40	14.9	1703-1897	194	1897
7. Fluffy 2	2a	4	88	31.6	1767-1985	218	1985
8. Fluffy 4	4	2	79	35.4	1678-1998	320	1998
9. Joseph 4	4a	2	55	15.0	1779-1998	219	1998
	4b	2	55	15.0	1728-1905	177	
	4c	2	55	15.0	1708-1988	280	
10. Vincent 3	3a	4	74	25.8	1823-1969	146	
	3b	4	74	25.8	1811-1989	178	1989
11. Brownie 1	1	4	62	28.2	1691-1905	214	1905
12. Brownie 4	4a	4	80	35.1	1816-1986	170	1986
	4b	4	80	35.1	1702-1810	108	
Western white pine (*Pinus monticola)*							
13. Her 3	3	5	94	37.3	1742-1985	243	1985
14. Vincent 2	2a	4	108	39.2	1729-1964	235	1964
15. Fluffy 1	1	4	88	31.6	1802-1979	177	1979
16. Bella 1	1a	4	55	48.7	1814-1920	106	
	1b	4	55	48.7	1800-1934	134	
	1c	4	55	48.7	1827-1939	112	1939
17. Bella 4	4	4	55	48.7	1849-1971	122	1971
18. Brownie 2	2	4	81	35.1	1760-1983	223	1983
	Mean		64.9	26.6			

Snags are therefore a persistent component of high-elevation coastal forests and individual species may decay and topple at markedly different rates.

The limited sampling of standing dead yellow-cedar trees in our study revealed ages since death that are similar to those reported for low-elevation western redcedar snags, even though dbh differs substantially between the two species (yellow-cedar mean dbh 62 cm (this study) vs. redcedar mean dbh 170 cm (Daniels et al. 1997). Various researchers have shown that small boles decay and topple more quickly than large boles (Cline et al. 1980, Graham and Cromack 1982). Hence, the difference in dbh suggests that snags at high elevations have a slower rate of decay and toppling than snags at lower elevations. This finding is consistent with predictions that snag decay rates are negatively influenced by increased precipitation (Harmon et al. 1987) and decreased temperature (Keenan et al. 1993), but the fungicidal properties of yellow-cedar may also play a role (Barton 1976).

Daniels et al. (1997) showed that decay class is weakly associated with age in low- and mid-

elevation forests of coastal British Columbia. The same appears to be true for the samples we collected in high-elevation forests at Mt. Cain, as shown by the wide range of ages within each decay class. Because of this poor association, we think it is unrealistic to predict either snag persistence or future snag population structure using the existing decay classification scheme. Prescriptions for the management of high-elevation forests should take into account the long persistence of snags and the high variation in decay rate among and within tree species.

Conclusions

Twenty-nine increment core samples from 18 high-elevation dead and dying trees were crossdated with living tree-ring chronologies to identify their time of death. Although our sample size was small, yellow-cedar trees appear to deteriorate slowly and can remain as standing snags for periods as long as 200 years. In contrast, the western hemlock and western white pine trees we sampled rarely remained standing for longer than 100 years. These findings highlight the persistence of standing dead and dying trees in high-elevation coastal forests and illustrate the difficulty in using a decay classification scheme for habitat management. Further research into moribundity, death, and decay of high-elevation trees should procure larger sample sizes of each tree species and decay class to firmly establish the range of possible snag ages. The full spectrum of old-growth coastal forest characteristics must be described if we are to develop adequate long-term management strategies for forests and their snag-dependant wildlife.

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Northwest Science Forum

Northwest Science Forum provides an opportunity to articulate and discuss scientific issues in a less structured format than peer-reviewed articles. The Forum publishes short articles, opinion pieces, and letters with a focus on science and natural resource issues in the Pacific Northwest. Although the Forum is not peer-reviewed, it is edited for format and clarity. Articles should generally be less than 2000 words and contain minimal literature citations. Letters in response to articles are particularly encouraged; the original author will normally be given a chance to respond to the letter as well. There are no page charges or reprints associated with the Forum, and participants need not be members of the Northwest Scientific Association. Please send all submissions, including two hard copies and an electronic copy (any recent version of Word or WordPerfect) to the Editor.

Dr. Jack Ward Thomas, Boone and Crockett Professor of Wildlife Conservation, The University of Montana

Watching the Columbia River Salmon Dwindle Toward Extinction—Elephants in the Room

(Speech given 17 March 2000 at Skamania Lodge, Stevenson, Washington)

Let me begin with the customary disclaimers. I am not an expert on salmon, nor am I as well informed on all the details surrounding the intricacies of the salmon's continuing decline in the Columbia River System as I would like.

Now, I follow with my "claimers." I spent some ten years of my professional career involved in high-profile roles dealing with spotted owl/old-growth issues in the Pacific Northwest. I was involved as a member—usually as team leader—of a series of task forces that started with the consideration of the welfare of a single sub-species (the Northern Spotted Owl) in a relatively specific habitat type (old growth forests) and ended up with a plan for ecosystem integrity. That plan included consideration of streams that harbored dwindling runs of salmon.

These efforts included the Interagency Scientific Committee (ISC), the so-called "Gang of Four," the Scientific Team (SAT), and the Forest Ecosystem Management Assessment Team (FEMAT). I then served three years as Chief of the Forest Service dealing with implementation of the Northwest Forest Plan. In that role, along with Dr. Michael Dombeck, who was Acting Director of the Bureau of Land Management, I ordered the Interior Columbia River Assessment. I had no idea that the effort would outlive my tenure as Chief.

I now spend my time as a professor, and have made one certain discovery in the process. I find that pontification is much easier and more fun than responsibility.

Those are my credentials for my pontification for today.

I also have some reputation as one who "tells it like it is," or, more likely, how I think it is at the moment. My impression is that I was invited to address you for that reason.

In preparing for this presentation, I made only a cursory review of the extant literature. But I did discuss my ideas with ten colleagues who are or were intimately involved, past and present, with the issue of salmon in the Columbia River System. None of them disagreed with the premise that I put before them, and encouraged me to "tell it like I think it is"—and added, "it is about time somebody did."

I think that many of the shortcomings in the current situation surrounding the welfare of salmon in the Columbia System are related to a failure to

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recognize that there are "elephants in the room." If that analogy does not ring a bell, I got it from a cartoon showing a group of people at a cocktail party blithely carrying on party conversation, ignoring the fact that the columns they were leaning against were the legs of elephants. If they recognized the elephants, they would have to react.

Look around you. Squint your eyes just a bit. The elephants are here.

I remember once being in a tour group that was on the Starkey Experimental Forest and Range on the Wallowa-Whitman National Forest in the Blue Mountains of northeastern Oregon. We stood on the banks of Meadow Creek, a tributary to the Grande Ronde River, which, in turn flowed into the Snake River. There were colleagues on the tour who remembered when there were salmon in Meadow Creek. No salmon now came back to Meadow Creek, though we were looking at a dramatically improved section of the stream. A short time earlier our research unit had been threatened with a "jeopardy call" because we were using a two-inch stubble height in the meadow to signal the time to move the cows. The National Marine Fisheries Service (NMFS) had dictated a three-inch stubble height. Someone asked me what I thought of the situation.

My reply went something like this: "As we stand here talking, the trawlers are working right off the mouth of the Columbia, and the sports fishing boats and their occupants are catching salmon. But we would not want to handle the economic, social, and political consequences of addressing that situation.

"Whatever salmon escape the nets and the hooks at sea start up the Columbia River and swim through the effluent from Portland and the settlements of the Willamette River. From this point forward they begin to encounter nets set by Native Americans fishing in concurrence with their treaty rights. A glance to either side of the river reveals an Interstate Highway and a parallel set of railroad tracks on one side and a double-lane road and a railroad on the other bank. There are dredges opening a channel for barge traffic. But, understandably enough, it would be tough to handle the economic, social, and political consequences of dealing with those limiting factors.

"And, whatever fish are left come to the first dam. Some get over the dam, and some don't. Then, the survivors swim through the tens of miles of slack water to the next dam, and the process is repeated. Some get over the dam, and some don't. This is repeated eleven times before the survivors can turn up the Grande Ronde River headed for the spawning gravels from which they emerged. But, clearly, we are not willing to face the social, political, and economic consequences of facing up to the problem associated with dams—particularly the dams in the lower river.

"As the fish proceed upstream they encounter agricultural areas where plowed fields stop only where they encounter the stream banks, and the runoff from the fields is laced with herbicides, insecticides, and fertilizer. Pumps pull irrigation water from the river and there are diversion ditches. Roads and railroads parallel the stream course for many of the miles from the mouth of the Grand Ronde River to Meadow Creek. Cows pound the stream banks on the private lands to the boundary of the Experimental Forest. But, clearly, we are not willing to face the social, political, and economic consequences of dealing with those problems.

"It is probably not necessary to go through this litany again to describe what the smolts will go through as they make their journey to the sea. And these would be the very few as might result from a chance encounter between what few salmon might make it back to the spawning gravels.

"So now we stand here and argue. We argue about whether the stubble height of three inches is so significantly different from that of two inches that a grazing experiment should be shut down in a riparian zone on a stream which has not had a single salmon return in 20-plus years. What is wrong this picture? Something had to be done somewhere to make it seem as if meaningful actions were underway somewhere. And so we were chosen. Why here? Why us? The answer seems simple enough to me. There were no social, economic, or political impacts of enough consequence to attract attention. We were relatively weak.

"We are not focusing on the real problems. We are taking on targets of opportunity, as regulators are demanded to do *something*, and it is directed toward those with relative lack of political clout."

Viewing the long term and continuing gyrations with the issue of saving salmon in the Columbia River System is, at the very least, not encouraging as far as long-term success is con-

cerned. Actions thus far are similar to the story described earlier, as new targets for action are chosen on the criteria of limited social, political, and economic impact. The rule seems to be: start with the weakest first, and move up the ladder as action is required.

Unfortunately, most of these efforts produce little or no result. For there is an elephant standing unseen in the room. That elephant is that the big problems, the *real* problems, are ignored as a matter of political expediency—or, perhaps, reality.

Simply put, as costs skyrocket, the Columbia River salmon continue to slide toward extinction. Simply put, as the struggle labors on to develop coherent policy and approaches between all the players—federal, state, tribal, quasi-public (not counting the myriad agencies at all levels)—the salmon continue to slide toward extinction. Simply put, as regulatory agencies, feeling forced to act under limiting factors, focus on players that are easy targets (and, regretfully, that are relatively insignificant to salmon recovery) and avoid dealing with the truly significant factors, the salmon continue to slide toward extinction.

One run of salmon after another "winks out" as the fish returning dwindle to zero in spite of the existence of spawning habitat. How, in the biological sense, is it possible that there can be any "take" by harvesting (i.e., killing) of salmon that might be upstream migrants in the Columbia System, headed for stream stretches where "wink out" is increasingly likely?

Clearly, managers are driven by the Endangered Species Act to carry out their roles in the prescribed drama, even if one failure after another is the consequence. I cannot think of another instance in the application of the Endangered Species Act where such ongoing failure would be tolerated. But, even that is not too hard to understand. The erstwhile "environmentalists" who took on the issues related to the northern spotted owls and other such tough fights simply do not have the heart for this one. They are willing to settle for incremental changes that address environmental issues piece by piece, whether or not truly related to salmon recovery. They cannot help but know that many of these actions are not likely to reverse the decline of the salmon, but will result in improvements in dealing with mine wastes, abusive grazing, roading, etc.

When they view the potential consequences of the suite of actions that would give salmon a real chance in the Columbia River System, they too ask that the cup be passed.

Let us examine just a few of the other elephants in the room as we ponder the fate of the salmon.

Examination of the purposes of the Endangered Species Act is in order: "The purposes of this Act are to provide a means whereby the ecosystems upon which endangered and threatened species may be conserved, to provide a program for the conservation of such endangered and threatened species . . ."

The Columbia River System has been so dramatically changed over the last century and a half—probably irreversibly—that "conservation" of the ecosystem in any semblance of its original state is simply not possible. Even draconian actions, such as removal of the lower Columbia dams, are almost certainly impossible due to astronomical direct costs and social, economic, and political consequences. Even cursory examination of dams, hatcheries, barging fish, dredging, roads, railroads, diversions, effluents from many varied sources, agriculture with associated pesticides, herbicides, and fertilizers, altered water flows, influences of urban development, and varied other impacts, quickly erase any vision of the protection of a long-gone ecosystem upon which threatened and endangered species depend. Many of the runs of salmon that still exist can be compared to a dying man essentially on full life-support—and still their numbers and range of occupancy dwindle. These pitiful remnants of what once was, not so long ago, but are no more except in dreams, are what Aldo Leopold called *numena*, or the spirits of a place.

For these wonderful creatures were the numena of the wild Columbia. The Columbia River of today is a working river. The economic, social, and political realities, I believe, assure that it will remain as such. Undoing of what has been done, except for a little cosmetic dab here and there, does not seem within the realm of the possible. The only parts of the ecosystem that are reasonably intact are the public land areas—and, oddly enough, (or perhaps understandably enough), they seem to receive most of the attention of regulators and planners.

Clearly, chances for survival of various runs of salmon are not equal. Many of the runs have

winked out, and the genetic make-up of the fishes in those runs is forever lost. Other runs continue in what appears to be an inexorable death spiral in spite of "best" (i.e., politically acceptable) efforts. Some runs are in reasonably good shape, and may well survive with appropriate management actions.

The perceived inflexibility in the ESA precludes the use of techniques to assign limited resources to those runs that have the best chance of maintenance and recovery, while ignoring those that are likely doomed. It is time to apply "triage" techniques, i.e., face up to what are likely irreversible declines in some runs in order to direct resources to those runs where the odds for long-term survival are better with adequate help.

Such an approach would also entail identifying land whose management can no longer be conceived as having an impact on salmon. Regulatory agencies should reduce their arena of activity to habitats that can realistically be identified as important to salmon welfare—and, simply put, leave other folks alone.

Costs of actions should be reported and recognized in a more realistic and comprehensive fashion. Costs are not limited to payrolls and expenditures. Both direct and opportunity costs are imposed on others—government and private—by regulatory actions. Frequently such costs are not accounted for and weighed in the balance. They should be.

The political process dealing with the salmon issue is hopelessly confused in spite of the best efforts of all involved parties. How could anything else be expected? Every entity involved has a different mandate, power base, constituency, objective, personality, source of funding, capability, vision of scale, and "boss."

I have absolutely no doubt that every "boss" is a person of good will, impeccable honesty, and dedication to do the "right thing." I have no doubt that every scientist involved from every agency and from every discipline is appropriately skilled and motivated to do the best possible job.

I am saying that the circumstances that exist could have been derived as a platform on which scripts for an old-time Keystone Cops comedy could be structured. In spite of all the good people involved, the circumstances do not bode well for either developing rational outcomes that will stand the test of ESA compliance, or that can be effectively executed.

If past is prologue, there may be lessons that can be derived from the experiences of dealing with the spotted owl/old growth/salmon "situation" (some might say "fiasco"). First off, it should be clear that the Columbia River salmon issue is far more complex—ecologically, politically, socially, legally, and administratively—than its predecessor crisis in the Pacific Northwest. Second, there are dramatic parallels in the amount of delay in developing a coordinated response and subsequent loss of options as various runs of salmon wink out. Third, the situation was allowed to fester until a series of teams were appointed that were given cover to work through appointment of a leader, who in turn was given the authority to work without political oversight to derive and evaluate options for a decision.

Scientists and technical support personnel must be chartered under a single leader with the authority and guts to face the situation—and defend the results. In my opinion, any such process that is guided by a "board of directors" from the various involved agencies will be so organized and conducted that it will produce a series of compromises before the time that such compromises should be made. Time frames will stretch as the team is sent back to the drawing board time after time for more analysis in hope of more politically viable answers.

Experience with the Interior Columbia Basin assessment effort indicates that to be the case—and reveals that more and more and more assessment does not produce significantly different results. In fact, more and more assessment and the time required produces rapid erosion of options for decision-makers. Threatened or endangered species are likely to suffer from delay, and chances for successful management dim accordingly.

However, continuing assessment and planning does make it appear that additional important and essential work is in progress—and, perhaps, even more research and assessment *is* essential prior to a decision. Maybe of greater importance for consideration is that drawn-out assessment and planning produce delays in making decisions that are to the detriment of threatened or endangered species, persons who will suffer as a result of the decisions, and politicians in whose back yards the decisions will have effect.

So there may be advantages to those who will be hurt or made miserable by change—and that makes up a considerable array. Delays can carry one beyond the next election, or, simply, put off the day of reckoning.

It may be time to ask: "What do we not understand about the salmon issues in the Columbia System that precludes coming to a reasoned conclusion?" The likely answer seems to be "not much."

In looking at the options that are currently under consideration, I find none that I believe would satisfy the intent of the ESA. Be that as it may, it seems likely that declines in some runs would continue, and some would wink out.

On top of that, I believe there is yet another very large elephant in the room. That is the question of who, finally, is to make the momentous decisions as to how much protection is afforded, and who takes the economic and social consequences. I do not believe that the continuing group grope of regional directors of various political entities and agencies "with a dog in the fight" will produce appropriate decisions. The mix of missions, mandates, pressure groups, constituencies, personalities, and political loyalties does not yield a suitable cultural medium for the growth of a solution.

Further, given the complexities surrounding the issues and the almost certain dramatic magnitude of the economic, social, ecological, and political impacts of any decision, I do not believe that this is a decision that should be made by a bureaucrat or a collection of bureaucrats. Given that the issue has international, interstate, and nation-to-nation connotations, and in view of the sheer magnitude of the impacts of that decision, there is one obvious choice for the decision-maker: the President of the United States.

There is a precedent for the President to make such a decision in a case of such dramatic import, and under strikingly similar circumstances. One of the ramifications of a decision by the President is that there are no appeals possible internal to the administrative branch of government, and the first step in opposition are the courts. Certainly, speed is of the essence in the case of the Columbia River salmon given the rate at which salmon runs are declining and the reduction of options implied in those losses.

Given the likely magnitude of economic and social consequences of any plan with any real chance of saving the salmon, the President would probably cut the finest possible line in choosing an option that would minimize impacts on human welfare while affording salmon a chance for survival. If the precedent of the Northwest Forest Plan held, legal actions from environmentalists and the tribes could be expected. These challenges would relate to charges of inadequate attention to salmon welfare. Those suffering economic damage would charge lack of adherence to process, inadequacy of data, inappropriate interpretation of data, or any other circumstances that would preclude institution of action under the chosen alternative.

A loss to the environmentalists or the tribes would require either more attention to salmon welfare, with associated increases in social/economic impacts, or an immediate appeal to the Endangered Species Committee (the "God Squad"). Either event would escalate the speed of resolution with associated savings in time, money, and options ("decision space" in the parlance of the planner.)

Congress, then, would be able to bless the decision by appropriating the funds necessary to execute the plan. Or, by refusing funding, veto the plan and open the door for a certain legal action for failure to adhere to the requirements of the ESA. Such a "veto" would run the risk of a judge-ordered action that could have dramatic impacts in the economy of the Northwest United States.

It seems implausible that the Congress would exercise such a "veto" without instituting legislation, predicated on the phrase "all other laws notwithstanding," that would legislate a solution to the impasse.

It does not seem possible that the Endangered Species Act was written, debated, and passed with any inkling that an issue of the magnitude of the Columbia salmon issue would arise. Magnified by the collateral issue of tribal fishing rights, this set of circumstances makes the spotted owl/old growth issue pale into relative simplicity and insignificance.

So I doubt that there will be any immediate overt recognition of the elephants in the room. But, if the elephants are not recognized and dealt with, there seems no room for bold strokes to come to grips with the issue to even be suggested. For, after all, it is said "the devil you know is better

than the devil you don't know." And, what official in his or her right mind, agency or political, would take a "lose-lose" situation of this magnitude?

The likely alternative of plodding on down the path that is being followed will likely produce continued diminution and wink outs of the salmon runs, a continued buildup in expenditures, accumulating restrictions on landowners (whether effective or not), and drawn-out assessments and evaluations. Declines in the fish runs may well continue as the inverse of expenditures, with no indication of cause-and-effect relationship.

Maybe it is time for someone to stand up and say loudly "Hold! Enough!"

This ongoing set of circumstances has taken on a life of its own, with its own cast of characters—and that cast routinely increases in size and costs. How many people's professional lives, how much occupational energy, how much political and social capital, and how much treasure (direct and opportunity costs) is it rational to spend in a losing game? The salmon continue their slide toward extinction, and options disappear as the runs wink out one by one—but the debate and disconnects with realities and costs continue to mount.

We have become too complacent, too accustomed to extant processes, too mired in those rituals, and too addicted to piecemeal "show piece" actions as the Columbia River salmon runs drift, seemingly inexorably, into the shadows known as history. There to become, for future generations, one of the myths of what once was in this land near the sea.

One of the first orders I gave when I became Chief of the Forest Service was to "tell the truth" and "obey the law." That made a lot of my fellows angry. I do not think, as a result, many paid much attention, and nothing changed much. But there is always hope. I thought it was good advice then and good advice now. So I repeat what I said then to you: tell the truth and obey the law.

The truth is that the situation for salmon is getting worse. The truth is that the situation is not likely to improve much unless we start breaching dams—and not just the four in the lower Snake River. The truth is that will occur when there is a really cold day in hell. The truth is that there is no acceptable way that we can come into compliance with the Endangered Species Act as it relates to salmon in the entire Columbia River System. The truth is that we are simply unwilling to come to grips with the issue that we have, probably irrevocably, decided that the Columbia River is a working river harnessed to provide the cheapest electrical energy in the world—and, simply, we ain't about to give that up. The truth is that playing games with various combinations of attempts to assuage limiting factors for the salmon will not do the job—and we know it.

If we frankly admit that we cannot obey the law, we are free to do the best we can to save the remnant populations. That can be done through a combination of directing money and resources to the places they will do the most good, and letting people off the hook who have nothing to do with those efforts. There should be no shame and much honor in facing the facts and telling it like it is.

We should do better. The law says so. Our professional ethics say so. Our consciences say so as we ponder what the Columbia River would be like without its numen. But in my opinion, we will do better only if we, very soon, recognize and deal with the elephants in the room.

Book Reviews

Terrestrial Ecoregions of North America: A Conservation Assessment.

Taylor H. Ricketts, Eric Dinerstein, David M. Olson, Colby J. Loucks, William Eichbaum, Dominick DellaSala, Kevin Kavanagh, Prashant Hedao, Patrick T. Hurley, Karen M. Karney, Robin Abell, and Steven Walters. 1999. Island Press. Washington, D.C. 486 pp. ISBN 1-55963-722-6, $75.00.

This book and its companion volume, *Freshwater Ecoregions of North America: A Conservation Assessment* reviewed below, are part of long-term efforts by the Conservation Science Program of the World Wildlife Fund–United States (WWF–US) to conduct conservation assessments of terrestrial, freshwater, and marine ecosystems around the world. These books are intended to serve scientists, students, professional and lay conservationists, and the interested public as current comprehensive conservation references. They can be considered the main authoritative references available on the status of terrestrial and freshwater ecoregions and offer guidance and sources of assistance to those interested in conservation and recovery activities. These comprehensive compendia are valuable additions to the conservation literature and deserve prominent positions in university, public, and personal libraries.

Originally, the authors from the WWF sought a single ecoregion framework to map terrestrial, freshwater, and marine biodiversity, however, differences in physical features, biogeography, species life histories, and levels of endemism precluded one definitive system for all ecoregions. For example, the natural distributional limits of species confined to freshwater systems correspond with larger drainage areas, lake margins, and spring locations. This pattern differs from terrestrial species distributions which are closely linked to vegetation, topography and soil type. In contrast, marine ecosystems in temperate and arctic zones differ from terrestrial ecoregions in that there are usually no fixed geologic or vegetative features that can be used to define ecoregion boundaries. In fact, the soon to be published volume on conservation assessment of marine ecoregions uses the distribution of organisms to differentiate between five ecoregions.

As a first step in prioritizing efforts to save terrestrial ecoregions, specifically the North American component of biodiversity, WWF–US and WWF Canada began a conservation assessment of the U.S. and Canada. Already, this authoritative material is being used by the conservation community in developing strategies for conserving biodiversity. The conservation assessment uses an index of "biological distinctiveness," which incorporates species richness, endemism, and other factors, and of "conservation status," including habitat loss, degree of existing protection, etc. By integrating these two indices, the conservation community can evaluate a combination of factors in each area and recommend appropriate conservation activities.

For terrestrial systems, the authors chose ecoregions rather than political jurisdictions for analysis because these provide a more biologically meaningful framework for biodiversity conservation and management. Broad-scale conservation is based on the concept that the maximum level of biodiversity is conserved when the maximum diversity of habitats are represented ublic and include suggestions of "measures to be taken." As well, the forty-five color maps artfully illustrate concepts and delineate areas of emphasis.

Appendices F and G comprise almost 60 percent of this book. In Appendix F are found individual descriptions of 116 ecoregions. This appendix introduces the environmental and biological setting of the ecoregion and summarizes the important factors that determine its ranking in broadscale analysis. Identified also are the remaining blocks of original habitat. authors found little peer-reviewed information on critical variables at the ecoregion level. To remedy this apparent paucity of published data, an experts' workshop was convened. Based on the collective experience and knowledge of the participants, standardized decisions were made. The rules and methods for calculating all criteria used in the decision-making process are available in the appendices. This

appendicized information clearly explains the process and ensures its repeatability. The assessment of biodiversity and threats to biodiversity was done only at a broad scale. However, the experts' workshop produced a wealth of information useful for designing approaches at finer scales, and this appendicized information benefits local initiatives.

Included in this compendium are nineteen special essays by knowledgeable individuals in the subject areas. These cover topics of major interest and in immediate need of attention. Essays are written in such a way that they can be easily understood by the general public and include suggestions of "measures to be taken." As well, the forty-five color maps artfully illustrate concepts and delineate areas of emphasis.

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As mentioned, assessments of freshwater biodiversity benefit from a separate set of ecoregions based on the zoogeographic patterns of the freshwater biota. The freshwater ecoregion assessment volume complements the terrestrial conservation assessment, since it considers the ways in which freshwater biodiversity conservation adds to and diverges from terrestrial-based efforts. The authors of the conservation assessment of freshwater ecoregions found that areas of unusual freshwater biodiversity are often not distinguished using terrestrial criteria; sometimes, special freshwater and terrestrial ecoregions overlap. However, threats facing terrestrial and aquatic systems often stem from the same activities, and well planned conservation activities may benefit biota in both realms.

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Freshwater Ecoregions of North America: A Conservation Assessment

Robin A. Abell, David M. Olson, Eric Dinerstein, Patrick T. Hurley, James T. Diggs, William Eichbaum, Steven Walters, Wesley Wettengel, Tom Allnutt, Colby J. Loucks, and Prashant Hedao. 2000. Island Press. Washington, D.C. 368 pp. ISBN 1-55963-734-X, $68.00.

Threats to freshwater species and habitats has attracted the notice of policy makers and the public, and support for conservation initiatives is growing. According to the WWF, nearly every freshwater system is suffering from some degree of degradation, and conservation resources are limited. This book was written to respond to the urgent and practical need for priority setting.

Freshwater ecoregions generally comprise aggregations of catchments, also known as watersheds or drainage basins. A catchment includes all of the land draining into a particular river (or lake, in the case of closed-basin systems) without exterior drainage. This conservation assessment uses an ecoregion-based methodology specifically tailored to freshwater systems. Instead of forcing freshwater species into a terrestrial framework, the authors adopted a more appropriate ecoregion-based scheme to more accurately reflect species patterns across the aquatic landscape. According to the authors, this is the first time a conservation assessment of freshwater biodiversity has been conducted using ecoregions derived specifically for freshwater species. Also, this is the first time that all of Mexico has been included in a North American assessment.

The authors' goals are to identify freshwater ecoregions that support globally outstanding biological diversity and to emphasize our global responsibilities to protect and restore them; to assess the types and immediacy of threats to North American ecoregions; to begin to identify specific sites within ecoregions where conservation activities may result in substantial benefits to biodiversity; to identify important information gaps that hamper an accurate evaluation of biodiversity; and to provide a broad-scale framework so that conservation agencies and other groups can place their activities within a continental and global context, resulting in more effective allocation of conservation resources. As mentioned, these objectives are similar to those guiding companion conservation assessments for terrestrial, marine, and freshwater ecoregions in North America, Latin America, and the Caribbean, Africa and Asia.

Similar to the volume on terrestrial ecoregions, the material in the book is divided into three main sections: the first outlines the approach used to make the assessment. More detailed descriptions of the specific methods and the scoring system for ecoregions are found in appendices (biological distinctiveness index, Appendix A and conservation status index, Appendix B). The second section includes results of the biological distinctiveness and conservation status assessments and the integration of indices into a priority-setting matrix. Raw scores for biological distinctiveness criteria (Appendix C), conservation status (Appendix D), and statistical analyses of the results (Appendix E) are provided. The integration of the two indices, conducted separately for each habitat type is also illustrated (Appendix F).

In the third section, the authors discuss major themes that emerged from the analyses. Interspersed throughout the results and discussion are 16 short essays providing supplementary information on topics in North American freshwater conservation. Final chapters provide a set of recommendations that, according to the authors, could enhance biodiversity conservation in North America and a glossary of important conservation terms for freshwater systems. Descriptions of all 76 ecoregions including ecoregion geographic extent, defining biological features, conservation status, analysis of threats, recommended suite of conservation activities, and contacts for conservation partners active in the region are in Appendix G. Lastly, Appendix H offers extensive information on possible conservation partners.

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The Oregon Weather Book: A State of Extremes

George H. Taylor and Raymond R. Hatton, Oregon State University Press, Corvallis, Oregon, 256 Pages. ISBN 0-87071-467-8. ($19.95)

and

The Climate of Oregon: From Rain Forest to Desert

George H. Taylor and Chris Hannan, Oregon State University Press, Corvallis, Oregon, 224 Pages. ISBN 0-87071-468-6 ($21.95)

Some of us that live in the Pacific Northwest actually look forward to winter, and the prospect of interesting weather. The generally quiet and pleasant conditions of summer bore us. We are thrilled and energized by wind, rain and snow and delight in reminiscing about unusual phenomena, especially storms. George Taylor and his co-authors clearly share this enthusiasm, and this affection for the weather of Oregon is imparted in their books *The Oregon Weather Book: A State of Extremes* and *The Climate of Oregon: From Rain Forest to Desert.*

The Oregon Weather Book concentrates on describing short-term weather related events with substantial societal impacts. These descriptions include both analysis of the events themselves, and discussion of the populace's response. The authors have done their homework, drawing from historical records to detail events going back to the 19th century. They show that it is generally large storm systems, with their attendant wind and rain or snow, that dominate the weather on the west side of the Cascades, while localized thunderstorms and their flash floods, constitute the main threat on the east side. *The Climate of Oregon* focuses on the contrasts between the typical weather found in various parts of the state. This is accomplished with a large number of maps and tables, along with narrative summaries. A sizable section is devoted to special topics, namely the effects of El Niño-Southern Oscillation (ENSO) on Oregon and perspectives on global warming. The two books include some overlap. The first section of each book, a short primer on weather, is identical. Their second sections, treatments of the elements of weather and climate, respectively, have considerable redundancy. They also share identical material on the collection and archival of weather observations.

There are a number of books available on Pacific Northwest weather, and it is worth considering how these offerings fit into that body of work. Most are largely tutorial in nature (recent examples include *The Wind Came All Ways* by Owen Lange; *Northwest Marine Weather Companion* and *Northwest Mountain Weather* by Jeff Renner) and are similar in many ways. They all discuss the large-scale structures associated with the weather, and how these structures are modified by regional to local sea-land contrasts and topography. But there has also been a book on the perceptions and adaptations to the weather of the Pacific Northwest, and especially Puget Sound, David Laskin's delightful and well-written *Rains All the Time*. While the present books are not unique in their nature or scope, they do fill a previously unexploited niche in their detail of the weather and climate of Oregon.

As a meteorologist living and working in the Pacific Northwest, I like to see correct explanations of our weather. In this regards, Taylor and co-authors do reasonably well, but there are some errors. For example, the climatological peak in precipitation in northern Washington occurs in December rather than October, graupel is not necessarily or even usually associated with subfreezing temperatures at the ground, and coastal upwelling is not due to merely the Coriolis effect but rather the interplay between Coriolis (rotational) and frictional effects. But these and other small errors due not materially detract. A more serious mistake was made in ascribing the winds in the Columbia gorge as a response to "funneling". The winds actually tend to be strongest downstream of the gorge's narrowest point; acceleration of the flow occurs through the entire length of the gap down the enhanced east-west pressure gradient that the Cascades help develop and maintain. There were also, arguably, some errors of omission. The segment on fronts could have benefited from discussion of how terrain and land-sea contrasts in the Pacific Northwest cause the weather associated with fronts to typically deviate from the usual conceptual model. An occasional, but important, wintertime forecast problem for the Portland area is whether there will be

snow or freezing rain, and it would have been appropriate to include something about the conditions that favor one versus the other. I was also surprised by the relative lack of mention of the strong winds along the coast that are typical in summer. One might imagine that the beach would be just the place to be on sunny summer afternoons, but that depends on one's tolerance to being sandblasted.

I feel strongly enough about the special topics section of *The Climate of Oregon* to give it some special attention here. The authors make an important and possibly under-appreciated point that the climate is not static, but that it changes due to various influences. Especially notable for the Pacific Northwest is ENSO, which accounts for virtually all of our present skill in seasonal weather forecasting for the region. But I must take issue with their discussion of the probability of global warming due to increasing concentrations of greenhouse gases. Taylor and Hannan argue that the evidence for present and future global warming is scanty. They select an unrepresentative sample of quotes to buttress their case (to their credit they acknowledge their personal bias). In fact, there is an emerging consensus to the contrary, as detailed in a recent book, *The Change in the Weather: People, Weather and the Science of Climate* by William K. Stevens, a science writer for the *New York Times.* On a local level, a recent report entitled "Impacts of Climate Variability and Change in the Pacific Northwest" from the Climate Impacts Group of the Joint Institute for the Study of the Atmosphere and Ocean (JISAO) describes how expected levels of warming will impact the Pacific Northwest, with particularly serious implications for summer water supplies and salmon stocks. The dismissal of the threat of global warming in *The Climate of Oregon* is shortsighted, in my opinion, in that it will just contribute to the public confusion regarding this issue.

Do I recommend these books? I expect that most weather enthusiasts in the Pacific Northwest, especially Oregonians, would relish *The Oregon Weather Book.* A couple of friends (neither meteorologists) were living in Eugene during the huge snowstorm of 1969. From their personal accounts, I assume they would like to read about, if not necessarily relive, that marvelous storm. Even newcomers to the region are liable to be impressed by how our normally benign weather can be punctuated by quite severe events. I am not as favorably disposed towards *The Climate of Oregon.* Setting aside my quarrel with their segment on global warming, I suppose that most people find climate less inherently dramatic, and hence as fascinating, as the day-to-day weather. In addition, a sizable portion of this book is taken up by tables with large amounts of specific information that will be of interest to few, and many of its maps suffer from a lack of contrast. That being said, it does complement the *The Oregon Weather Book,* and I tip my hat to Taylor and his co-authors for putting together a pair of books that should find a substantial and interested audience.

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Flora of Mount Rainier National Park

David Biek, 2000, Oregon State University Press, Corvallis, Oregon, 520 Pages. ISBN 0-87071-470-8. Paperback, ($29.94)

At last, we have a definitive, up-to-date flora of Washington's oldest park, Mount Rainier National Park. The last such flora was that of George Neville Jones, *The Flowering Plants and Ferns of Mount Rainier.* It contained 729 species, while the present work by Biek has a total of 851 species; this larger number includes both newly introduced exotics as well as new finds of native species. The only other fairly complete flora was that of C. Frank Brockman, *Flora of Mount Rainier National Park* (1947). Therefore, a thorough revisional treatment of the Park's flora is most welcome. Not only is the present work an expanded version, it has included the many changes of botanical names that continue to appear. It is well to point out that Biek's volume will serve well for seekers of plant identifications in most other areas of the Washington Cascades.

The author, David Biek, has an unusual background for carrying out his tryst with the plants of our great volcanic mountain. He is a librarian with the Tacoma Public Library. One may opine that librarians and catalogers of floras do have similar skills. Then, it also goes to show what a competent "amateur" (a lover of a pursuit . . . not a professional) can create out of a love of a place and its plant life. Biek has fashioned a masterful, professional rendition of the Park's flora.

The first twenty-five pages, preceding the flora proper, give the user valuable insights on the Park's natural history: its topography, climate, and several major plant communities, from lowland to the alpine. He further indulges in a section on weeds, the aliens that "thrive under human disturbance." Finally, Biek gives us a thoroughgoing account of the history of botanical collecting in the park, from William F. Tolmie of Hudson's Bay Company at Fort Nisqually to the many contemporary collectors like J.W. Thompson and J.R. Slater of the University of Puget Sound.

The balance of this indispensable field guide is devoted to the flora itself; nearly 500 pages of flora, with keys to the families, genera, and species; the text embraces ferns and their allies, conifers and flowering plants. Each species is described in easy to fathom terms, with a minimum of botanical jargon. For each, a good diagnostic line drawing is provided; these are the superb drawings by Jeanne Janish that first graced the pages of the monumental Pacific Northwest floras by Hitchcock, et al. (1955–1969, 1978). Accurate accounts of a plant's habitat are given along with useful specific localities for each. There are also eight pages of colored photo close-ups of selected plants. The publisher could have done a better job of rendering them; some are unclear and all are a bit washed out.

This reviewer was attracted to the author's treatment of the ferns. Not only the common ones are well done; Biek gives attention to some of the rare ones, like *Polystichum andersonii, P. kruckebergii, P. imbricans,* and *Cryptogramma cascadensis*. And the fern nomenclature is quite current, as is that of other species in the flora. The author has been very astute and faithful to the most recent treatments of such difficult genera as *Castilleja* (the paintbrushes), *Penstemon* and *Carex* (41 species!). Besides giving authorship to each botanical name, Biek assures that each plant has a common name (41 for the sedges!).

Biek treats the Rainier flora in a "user-friendly" way. The keys are easy to use and the families, genera, and species are arranged alphabetically in each category. For the few technical terms he uses, one will find a handy glossary just before the index.

I highly recommend this thoroughly professional, complete, yet handy field guide. It is portable, yet not skimpy in its full treatment of the Mount Rainier flora. It is worth mentioning again that it should be quite useable beyond the Park, most anywhere in the North Cascades.

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Narrative of a Journey Across the Rocky Mountains to the Columbia River

John Kirk Townsend (Introduction and Annotation George A. Jobanek), Oregon State University Press, Corvallis, Oregon, 290 pages + i-xxix. ISBN 0-87071-525-9, $16.95

Students of natural history often refer to two ages of discovery in North America: the first being the time from European settlement until the early 1800s during which much of the flora and fauna of the eastern United States were described; and the second beginning in1804 with the westward trek by Lewis and Clark and the subsequent description of hundreds of western species previously unknown to science. John Kirk Townsend was a leader in the second age of discovery. Modern science education programs give little attention to either the naturalists who collected and described new species across the North American Continent, or to the extraordinary efforts (and competition!) involved in their collections, journeys, and expeditions. This book provides substantive information on both the man and the circumstances surrounding the discoveries by John K. Townsend.

This book is part of the Northwest Reprints Series, edited by Robert J. Frank, in which nineteen classic works from the region's past have been reprinted for the modern audience. This reprinted *Narrative* is the first full treatment of Townsend's seminal work since its original publication in 1839. The book is true to the original *Narrative* in spelling (and misspelling) , punctuation, and grammar. The title is somewhat misleading, in that the Journey includes a "side trip" for several months in the Hawaiian Islands ("Honoruru"), a return to Fort Vancouver at the mouth of the Columbia, and the voyage back to Philadelphia via Hawaii, Tahiti, Chile, and around Cape Horn.

This is a handsome book. The soft cover is graced by a Townsend's warbler superimposed on an early map of much of what is now Washington state. The warbler is one of several species that Townsend was the first to collect for science during this journey.

The book contains a long, but very informative introduction, eighteen chapters, an appendix listing the species encountered during the journey and the subsequent published scientific descriptions, and ends with a thorough annotated bibliography.

The nineteen-page introduction by George A. Jobanek, author of *An Annotated Bibliography of Oregon Bird Literature Published Before 1935* (OSU Press) not only excerpts some of the high points of the expedition, but gives a crisp biography of Townsend both before and after the journey. It paints a picture of young Townsend as a somewhat privileged and engaging young man, extremely skilled in the art of conversation, and often invited into the homes of high society. In 1934, at age twenty-four, Townsend held a Doctor of Science Degree, was living in Philadelphia (then the center of natural science in North America), and was close personal friends with legends James J. Audubon and Thomas Nuttall. By a sequence of who knows whom, Townsend became the first trained naturalist, along with Nuttall, to traverse the continent with the specific intent to collect western species for science. In April 1834 the Columbia River Fishing and Trading Company expedition, under the leadership of Nathaniel J. Wyeth, embarked from Independence, Missouri for Fort Vancouver, at the mouth of the Columbia River, with 58 men, among whom were Townsend and Nuttall, two Methodist Missionaries, and trappers, guides, trackers, hunters, and others associated with Wyeth's company. Included was Osborne Russell, who later achieved modest fame for his accounts *Journal of a Trapper (1834-1843).*

Because the writing of the *Narrative* occurred more than a century and a half ago, the language is in the style of the early part of the nineteenth century: flowery, frequently verbose, and often requiring a second read to comprehend. Nevertheless, the language only adds to the account, carrying the reader back in time, and providing a constant reminder that, for the times, this journey was indeed an adventure of grand proportions.

Although Townsend's journal is a daily diary, the text does not ramble and wander into dead ends like many other pioneer diaries. With few exceptions, each entry contributes to the narrative. It appears Townsend spent some time thinking about and organizing what he was going to write before putting pen to paper. His descriptions of travel and camp life are enlightening and not without occasional humor. He describes all

matter of physical and emotional discomfort (including the loss of the first volume of his journal while crossing a river!) in a resigned, matter-of-fact tone, which continues to remind the reader that this is an account of an earlier time when life was much closer to the ground.

To me, the major disappointment in the journal was the scant attention actually given to natural history. Townsend was a professional naturalist, but he does a meager job of exciting the reader about new biological discoveries ("Collected about 80 specimens today, many of them new."), and presents habitat descriptions from a most practical viewpoint ("The grass is dry and poor."). For the anthropologist, and general historian, though, this narrative is a treasure. Townsend provides detailed descriptions (usually less than complimentary) of most of the aboriginal peoples encountered along the way. He captures the essence of their clothing, customs, habitation, and habits. He seemed particularly fond of descriptions of the shape of the skulls, especially after meeting several of the Pacific Northwest tribes whose cultural tradition included molding the head shape of infants.

His side trip to Hawaii, mostly to get away from the dreary and miserable winter conditions at the mouth of the Columbia River, is a wonderful interlude. Here he and Nuttall are befriended by the King and treated like royalty. Townsend's description of the island peoples, daily life, and the juxtaposition of pagan ceremony and missionary religion are enlightening.

At first reading, the appendix, containing the list of species encountered and the published accounts introducing new species to science, was a letdown. The lists seem unexpectedly small and the scientific accounts lacked any quantitative information, useful physical measurements, and discussion of habitat affinity and or behavior. This was a disappointment until I realized I was evaluating these achievements by today's standards, when I should have remembered these descriptions were written when keen observation and attention to visual detail were the keystone of natural science, with the disciplines of biostatistics, ecology, and even the scientific method, still decades in the future.

Overall, I found the narrative interesting and informative. Townsend's comments about aboriginal peoples would not be acceptable in today's writings, but if you can keep his comments in the historical perspective of Western exploration more than a century and a half ago, this was a most enjoyable journal.

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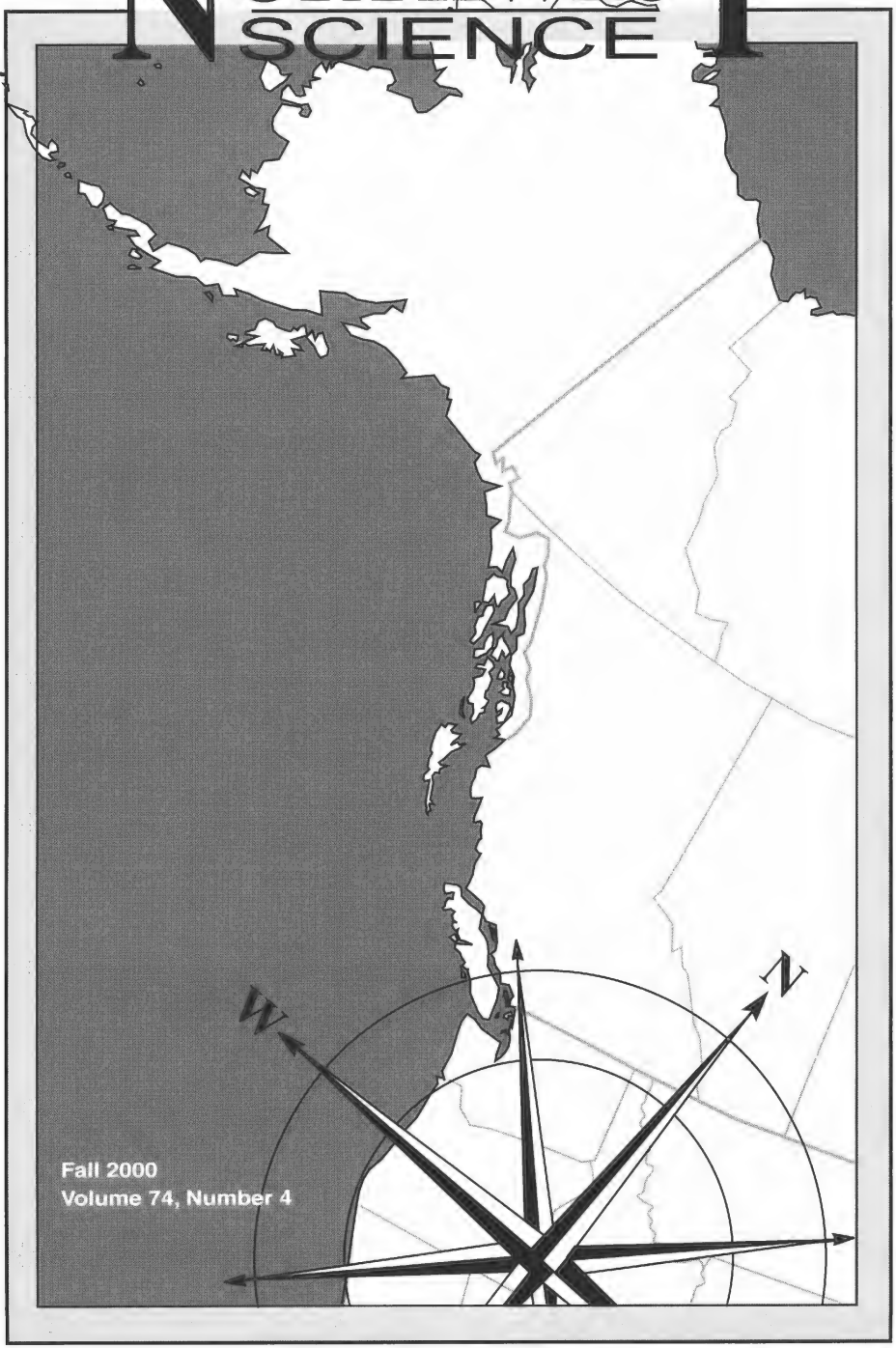

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Announcements

Annual Meeting, Humboldt State University, March 21-24, 2001

The 74th annual meeting of the Northwest Scientific Association will be hosted by Humboldt State University in Arcata California from Wednesday March 21 to Saturday March 24, 2001. Following a business meeting of the governing board on March 21, scientific sessions and field trips will occur on the following three days with a variety of concurrent sessions and symposia. Redwoods National and State parks will hold sessions on research in parks and the Institute for Forest Canopy Research at Humboldt State University will be holding a session on forest canopy biology. In Addition, the Northwest Lichen Guild and the California Society will be joining the meeting and hold sessions on lichens as well as a taxonomy workshop on the genus *Usnea.* Bob Van Pelt and Steve Sillett will lead a Saturday field trip to several of the finest old-growth redwood forests in Redwood National and State Parks. The focus will be on BIG TREES!

Members and nonmembers are welcome at the meetings, and students are especially encouraged to attend and report results of their research. Anyone interested in helping to organize or chair sessions should contact Steve Sillett, Department of Biological Sciences, Humboldt State University, Arcata, CA 95521. Phone: 707-826-4167. Fax: 707-826-3201. E-mail: scs6@axe.humboldt.edu. Steve is looking for help to make this a great meeting – so step forward. A call for abstracts and meeting registration information will be mailed to all members of the Northwest Scientific Association.

Northwest Scientific Association 2001 Student Research Grant Competition

The Northwest Scientific Association annually awards grants of up to $1000 to support student research. Applicants must be student members of the Northwest Scientific Association (see inside front cover of *Northwest Science* for membership application information). Four copies of the proposal must be received on or before 1 February, 2001, and sent by surface mail to:

Dr. A. Ross Black
Department of Biology (Sci 258)
526 5th Street
Eastern Washington University
Cheney, WA 99004

Proposals should include (in the following order): 1) a cover page which provides the project title, name and address of the student applicant (including phone number and e-mail address), name of the major professor or advisor, and the dollar amount requested; 2) an itemized budget ($1000 max.); 3) the body of the proposal which provides a specific statement of the project goal(s), the background, justification, appropriate preliminary results, and the project methods (including experimental design, methodologies, appropriate statistical analyses, and timeline); 4) literature cited; and 5) supplementary tables and figures. The body of the proposal is limited to no more than four pages of double spaced text in 12-pt font with one inch margins (excluding title page, budget, literature cited, and supplementary tables and figures).

Awards provided by the Northwest Scientific Association are intended to support student researchers in the pure and applied sciences. Monies can only be used to support travel, equipment, and supplies for student research (proposals requesting salary support will not be considered). Recipients are required to present the results of their research at a future Northwest Science meeting. NWS will waive page charges if grant recipients choose to publish their research in *Northwest Science* within four years of accepting their grant. Grant winners will be announced at the 2001 NSA annual meeting at Humboldt State University. Questions concerning grant application procedures should be directed to Dr. Ross Black via e-mail (rblack@ewu.edu).

Minutes of the Annual Meeting, March 16, 2000, Moscow, Idaho

Paul McDaniel announced that President Ted Thomas would be late due to travel delays. The board agreed that Tim Reynolds, President-elect, would chair the meeting.

President-elect Tim Reynolds called the Spring 2000 Board Meeting to order at 4:09 PM.

PRESENT: Barry Keller, Kurt Othberg, Steve Rust; Sarah Greene, Steve Acker, Dave Hansen, Len Broberg, Ken Kardong, Nancy Grunewald, Tim Reynolds, Ed Schreiner, Paul McDaniel, and Peggy O'Connell

ABSENT: Ross Black, Steve Sillett, John Koprowski, and Darlene Zabowski.

MINUTES AND SECRETARY'S REPORT: Margaret O'Connell read the minutes from the 16 October 1999 Fall Board Meeting. The minutes were approved. She announced that an update of the Governing Board Manual is planned. She reported that all correspondence with AAAS was up to date.

TREASURER'S REPORT: Dave Hansen gave the Treasurer's Report. Last year's meeting in Tacoma broke even. Total assets are at $50,536.29. NWSA has 353 total members (ca. 30-40 student; 40 sustaining, 22 life members). Total number is down from a high 450 several years ago. The report was approved.

EDITOR'S REPORT: Ed Schreiner passed out new journals. The journal has averaged 44-45 submissions/year; this past year 65/year. First quarter we have already exceeded our first quarter trends. Ed Schreiner has cleaned up instructions for authors. As of next March—Ed Schreiner will be stepping down—end of three-year term. He is looking for replacement. He is writing information for new editor. The board recognized Ed Schreiner's hard and conscientious work with a round of applause.

HONORS AND AWARDS: The committee reported that four nominations for Outstanding Scientist were received. The committee selected John C. Tappener—forest ecologist from Oregon State University. The committee recommended David Hansen for Honorary Life Membership. Both motions for awards carried.

STUDENT AWARDS: The Student Awards Committee reviewed 27 proposals and awarded three. The three awards went to:

1) Brian B. Oakley—U of Washington—College of Forest Resources. Effects of experimental burn treatments on soil N availability ($972);

2) Sunny Bennett—Humboldt State University—Department of Biological Sciences. The effects of fire on epiphytic lichens and bryophytes on *Quercus garryana* in Redwood National Park, California ($1000);

3) Colden Baxter—Oregon State University—Dept. of Fisheries and Wildlife. Longitudinal patterns in fish assemblages and stream habitat relationships: temporal dynamics and the role of migration in a Pacific Northwest river ($1,000).

The committee's recommendations were approved. The deadline for submitting proposals for next year will be 15 January 2001. All student members are encouraged to do so.

NOMINATING COMMITTEE: The Nominating Committee presented its nominations for officers and trustees. Tim Reynolds will be president 2000-2002. Theodore Thomas will rotate as past-president. New nominations: Douglas Call (formerly Battelle, now WSU), Dan Stephens (Wenatchee Valley College), and James R. Belthoff (Boise State University). There are still two openings on the board and members were encouraged to volunteer or submit names. [note: these positions were later filled by Joanna Schultz (Lewis-Clark State College) and Karl Lilquist (CWU).

ANNUAL MEETINGS: Paul McDaniel reported that 50 people had pre-registered for the 2000 Meetings. This is low compared to recent years. We have 40 presentations that have been submitted. The 2001 Meetings will be held at Humboldt State University in Arcata, California. The board stressed the value of joint meetings with other societies.

The meeting was adjourned at 6:30 PM.

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and

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Fire History of Douglas-fir Forests in the Morse Creek Drainage of Olympic National Park, Washington

Abstract

In the Morse Creek drainage of the northeastern Olympic Mountains, montane forests dominated by Douglas-fir owe their prominence to a complex fire regime that incorporates high severity stand-replacing fires and low/moderate severity ground fires. We quantified the fire history of these forests to determine the role played by wildfire to favor dominance of Douglas-fir rather than late-successional western hemlock. Three matrix forest types reflect the influence of past wildfires. The youngest matrix type was <150 yr old, next was a matrix type 150-300 yr old, and the oldest was >300 yr old. Germination dates and fire release markers were identified on increment cores from 318 Douglas-firs, and used to date past fire events. A 600-yr fire history was developed for this 2500 ha area. Periods characterized by many small-scale, low and moderate severity fires were interrupted by two high severity, stand-replacing burning periods in 1687-1720 and 1897-1904. Mean fire return intervals (FRI) were calculated for various land units. The most informative size was 200 ha, the approximate mean size of lateral tributaries to Morse Creek. FRI was 21 yr at this spatial scale. For the entire 2500 ha drainage, mean FRI was estimated at 3 yr. Similar to Douglas-fir forests in central Oregon and northern California, small patchy fires were much more common in the eastern Olympics than previously thought. Instead of fire exclusion, a policy that uses management fires to burn many small patches of forest each year would approach the kind of fire regime typical of these forests.

Introduction

Forests in the Pacific Northwest support three different fire regimes, based on fire severity (Agee 1993). Low severity fires are surface fires that kill a small percentage of the tree species on the site. High severity fires are canopy fires that kill a high percentage of species. Moderate severity fires define a broad range between these two extremes, such that some of the species are killed by a fire whereas others survive. Authors writing about western fire regimes often simplify the discussion by contrasting low severity fire regimes with high severity fire regimes (Kilgore and Taylor 1979, Arno 1980, Swetnam and Dieterich 1983, Schullery 1989, Greenlee and Langenheim 1990, Stephenson et al. 1991, Swetnam 1993, Agee 1997), but all three fire types can burn in Pacific Northwest forests (Agee et al. 1990, Morrison and Swanson 1990, Wallin et al. 1996, Cissel et al. 1998, Taylor and Skinner 1998). The proportions accounted for by each fire type vary depending on the vegetation type under consideration, climate, fire weather, and fuel accumulation (Agee 1993). Over several centuries, the combined differences in fire severity have created a mosaic forest structure at the landscape level, with patches of forest reflecting low, moderate, and high severity fires (Morrison and Swanson 1990, Stephenson et al. 1991).

Mean fire return interval (FRI) is the mean time span between fires, specific to a given unit of land, vegetation type, or region. FRI have been studied by many workers in the western United States, using units of land varying in size from a single tree (<0.001 ha) to entire watersheds (>600 ha)(Kilgore and Taylor 1979, Madany and West 1980, Arno and Peterson 1983, Swetnam and Dieterich 1983, Cooper et al. 1987, Barrett and Arno 1988, Agee et al. 1990, Morrison and Swanson 1990, Taylor and Skinner 1998, Brown et al. 1999, Taylor 2000). FRI provide fundamental information about the fire history of a region, and fire severity can be inferred from FRI. Communities with shorter FRI generally are characterized by low and moderate severity fires, because fuel loads accumulated between fires are insufficient to support crown fires, even under extreme fire weather. Communities with longer FRI generally are characterized by high severity fires during extreme fire weather, which are supported by the high fuel loads accumulated between infrequent fires.

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Douglas-fir (*Pseudotsuga menziesii*) dominates montane forests west of the crest of the Cascade Range from northern California to Washington. Fire has been an important environmental factor throughout this region, and the widespread dominance of Douglas-fir is testimony to its ability to respond positively to low, moderate, and high severity fire regimes. When mature, Douglas-fir is a resister to low and moderate intensity fires (Agee 1993). Since Douglas-fir commonly repopulates sites cleared by stand-replacement fires, it is an invader in high intensity fire regimes. When young, Douglas-fir is sensitive to fire, and is classified as an avoider (Agee 1993).

For over half a century, Douglas-fir forests on the Pacific slope have been understood to support infrequent, high intensity, stand-replacement fires (Munger 1940, Fonda and Bliss 1969, Hemstrom and Franklin 1982, Henderson et al. 1989, Agee 1997). FRI of 200-400 or more years were commonly estimated for Douglas-fir forests in the Pacific Northwest, largely based on dates of stand establishment after high severity fire. Research in Douglas-fir forests since 1990, however, has revealed that fire frequency is much shorter, and fire severity is much less, than previously thought. The central Cascade Range, Oregon, has been the most intensively studied region, and Douglas-fir forests there support low, moderate, and high severity fire regimes (Morrison and Swanson 1990, Wallin et al. 1996, Cissel et al. 1998). In this region, the well-known 200-400 yr FRI resulted in large, stand-replacement fires, however, many old growth stands in the study area resulted from multiple, patchy fires of varying severity, with 20-100 yr FRI (Morrison and Swanson 1990). Data from Wallin et al. (1996) and Cissel et al. (1998) agree with this general pattern. Forests in the Klamath Mountains, California, support a complex fire regime characterized by frequent, less severe fires, with FRI ranging from 13-22 yr (Taylor and Skinner 1998). These forests differ from the northern Douglas-fir forests, however, because a mixture of overstory conifers with a more flammable understory characterize the stands. Both the central Cascades and the Klamath Mountains support multi-aged stands, products of low and moderate severity fires, and even-aged stands, products of high severity, stand-replacement fires (Morrison and Swanson 1990, Taylor and Skinner 1998). Mean FRI of 7-9 yr at Point Reyes, California, are the shortest yet reported for Douglas-fir forests (Brown et al. 1999). Clearly, the fire regime associated with forests dominated by Douglas-fir is much more complex than originally reported.

The northeastern Olympic Mountains lie in a rain shadow that produces some of the driest conditions north of California. In this region, montane forests are dominated by Douglas-fir stands initiated after past fire events (Fonda and Bliss 1969). Even-aged stands grow where high severity crown fires burned; uneven-aged stands with multi-story structure remain where low severity fires burned (Pickford et al. 1977, Franklin and Dyrness 1988), and they contain occasional fire survivors >1000 yr old (Henderson et al. 1989). Fire weather, lightning patterns, and fuel loading govern fire size in Olympic National Park (Pickford et al. 1980). Ignitions are governed primarily by fire weather and fuel moisture, secondarily by available fuel. If extreme fire weather dominates the region, and fuel moisture is low, ignition causes high severity crown fires (Agee 1997) that burn uniformly through the forest. Fuel moisture, however, is rarely low enough to support stand-replacement fires. If fires start under less than extreme conditions, ignitions cause low severity surface fires that burn in patchy patterns. Of the five fire regimes described by Stephenson et al. (1991), two apply to the general fire regime of the eastern Olympics: 1) high intensity fire with patchy low intensity fire, for which groups of canopy trees survive within a matrix of dead trees; 2) uniform high intensity fire, for which the majority of the canopy trees are killed. For eastern Olympic montane forests, FRI has been estimated at 270-300 yr (Fonda and Bliss 1969), 200-300 yr (Fonda 1979), and 130-250 yr (Henderson et al. 1989). These estimates, applied specifically to high severity fire episodes in the montane zone, were derived from stand establishment dates. Each reflects the common clusters of postfire establishment dates, and possibly maximum tree ages, associated with the forests studied, but none specified the units of land to which FRI applied.

No fire history studies in the eastern Olympics have investigated the possibility of a complex fire regime of low, moderate, and high severity fires, nor have any studies related FRI values of Douglas-fir forests to specific units of land. In this study, we quantified the fire history of the Maiden Creek tributary of Morse Creek in the

northeastern Olympics. We wanted to calculate FRI to determine the relative proportion of frequent, low/moderate severity fires and infrequent, high severity fires. We asked four research questions: 1) has fire favored dominance of Douglas-fir in this drainage, rather than the late-successional western hemlock (*Tsuga heterophylla*), as occurs elsewhere on the Olympic Peninsula (e.g., Fonda and Bliss 1969, Henderson et al. 1989)? 2) what are the age and structure of stands in the Morse Creek drainage? 3) when did widespread, high severity fires burn compared to smaller low and moderate intensity fires? 4) what are the modal characteristics and ranges of the fire regime in this region?

Methods

The study site was in the Morse Creek drainage, south of Port Angeles, Washington. We concentrated on the section of the drainage defined by Maiden Creek and by Morse Creek near the confluence with Maiden Creek. Topographically, the area is characterized by steep slopes falling 350-750 m from the forested ridge lines to Maiden Creek and Morse Creek (Fig. 1). Morse Creek's lowest elevation in the study area is ~325 m. Maiden Creek's upper elevation in the study area is ~1050 m. Forest stands in the montane zone of the drainage are dominated by Douglas-fir, with various amounts of western hemlock (Fonda and Bliss 1969). High severity fires in the montane zone of the Olympics kill nearly all trees (Fonda and Bliss 1969, Henderson et al. 1989), although a few trees may survive (Fig. 2). In this paper, we apply the term matrix forest types to stands that develop after the fire, but which can contain a few survivor trees. The age of the matrix type is defined by the ages of the postfire trees, not the older survivor trees. Our study identified matrix types and survivor trees in the montane zone. Above this zone, at ~1200 m, is the subalpine forest zone, characterized by stands dominated by subalpine fir (*Abies lasiocarpa*), and a few localized stands of lodgepole pine (*Pinus contorta*) dating from fires near 1900 (Fonda and Bliss 1969, Zolbrod and Peterson 1999).

We constructed the fire history of this drainage from two databases: 1) age classes of matrix types established after a high severity fire, based on germination dates of trees assumed to have germinated in response to that fire (Figs. 1, 2); and 2) fire release markers (Fig. 3) in cores taken

Figure 1. View south from Mt. Angeles into the eastern portion of the study area and Maiden Creek. Forests responding to fires within the past century have smooth, fine-grained-appearing canopies. Forests responding to older fires have rough, coarse-grained canopies.

from trees that germinated in response to high severity fires 250-500 or more years ago, and that survived subsequent fires (Fig. 2).

All trees were bored ~1.4 m above the root collar on the upslope side of the tree during summer 1994. Diameters of trees within 38 groves were measured at 1.4 m (i.e., dbh), the trees were bored, and the cores were stored in labeled straws. We bored >700 living trees. Many of the Douglas-firs sampled were at least 250 yr old, but various fungal pathogens made more than half the cores extracted unusable for this study. All trees used for analysis were alive when bored, and we assumed that the outer ring was from 1994.

Increment cores were mounted on boards, then sanded smooth with progressively finer grit to expose annual growth rings. Abrupt and sustained increases in ring width (Fig. 3) were determined with an ocular micrometer integrated into a 6-40X

Figure 2. Two survivor Douglas-fir trees, >300 yr old, in a 90-yr Douglas-fir stand (DF1). The high tree density and mortality are typical of the DF1 matrix type.

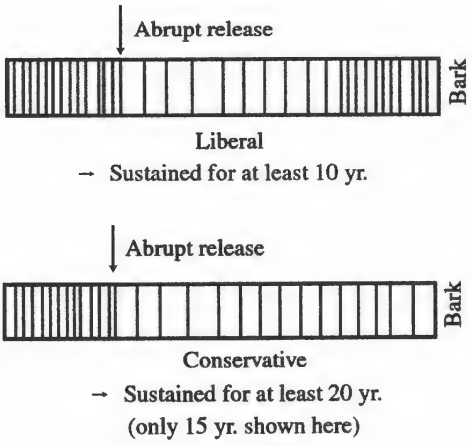

Figure 3. Examples of fire release markers. Liberal releases are based on 10 yr of sustained growth, as shown. Conservative releases are based on 20 yr of sustained growth, although only 15 yr are shown in this example.

stereoscope. These growth releases were associated with past fires, and they were judged on each core according to liberal and conservative criteria (Fig. 3). A release classified as meeting the liberal criterion showed an abrupt increase in ring width, with subsequent growth sustained for over 10 yr. Conservative releases showed at least a fivefold increase in measured ring width over the previous year, with subsequent growth sustained for at least 20 yr.

All increment cores in this study were scored separately by two people. Each person evaluated each core twice, first to identify liberal release patterns and again to identify conservative release patterns (Fig. 3). Cores with dates about which the two disagreed were completely reevaluated until the disagreement was resolved. Ultimately the pith age at 1.4 m of every tree core was accurately determined, and accurate dates were assigned to the growth releases.

We ensured that the dates associated with events recorded in our tree cores were visually accurate, but we did not attempt to match ring patterns among the 318 cores we obtained. We sampled trees from the forest interior, and they had the characteristics of the complacent tree-ring series (Fritts 1966, 1971; Stokes and Smiley 1968). In contrast to the sensitive series, tree-rings in the complacent series are uniformly wide, with low correlation among trees. The standard deviation associated with ring widths on individual cores is low (Fritts 1966, 1971), and the lack of variation is unlikely to produce useful sequences (Stokes and Smiley 1968). Brown et al. (1999) faced exactly this situation with fire scar data from Douglas-fir in California. In the forest interior, precipitation is effective from year to year, there is less variability in annual precipitation, and fewer days when moisture is limiting (Fritts 1966, 1971). Thus, the trees are unlikely to have missing rings, especially in northern climates (Fritts 1971). Missing rings in Douglas-fir are uncommon west of the Cascade Mountains in Washington, and are a negligible source of error in establishing the age of the tree and fire events (Morrison and Swanson 1990). We assumed the trees in the study area had no missing rings and they presented a complete record of the age and history of the trees.

In drier mountainous regions, Douglas-fir and ponderosa pine (*Pinus ponderosa*) are resisters to low intensity fires (Agee 1993), and both exhibit

visible injuries in the form of cat-faces with associated fire scars. Douglas-fir that survive fires in the Olympic Mountains lack cat-faces and visible fire scars, however, their responses to fire can be recognized by release markers in the growth rings (Fig. 3). Fires that kill neighboring trees open the canopy of the stand, providing an improved growing environment for surviving trees (Stephenson et al. 1991). The improved growth is recorded in tree-rings in years subsequent to the fire event (Morrison and Swanson 1990, Stephenson et al. 1991, Swetnam 1993, Mutch and Swetnam 1995). We assumed that the wood of trees recording fires by growth release markers was uninjured by the fire. Still, fire may scorch foliage and bark (Mutch and Swetnam 1995), and injure fine roots (Swezy and Agee 1991). Damaged trees might respond to high severity fires initially with decreased growth for up to 2 yr (Morrison and Swanson 1990, Mutch and Swetnam 1995), although subsequent growth increases are possible beginning in the third year (Mutch and Swetnam 1995). To account for possible lags between fire and the growth release, we adjusted fire dates for cohort trees within the same grove and likely fire perimeter that had markers within 3 yr of each other to the earliest fire date within the period in question.

Conversely, it is possible that a larger growth ring could be the result of a canopy gap created by wind throw. Morrison and Swanson (1990) acknowledged this relationship, but discounted the importance of wind relative to fire. They noted that stands disturbed by wind were locally small, and had a low abundance of early seral tree species in these areas. In our study area, the Douglas-fir matrix surrounding any witness tree was more extensive than could be accounted for by wind throw. Furthermore, the 460 growth releases recorded by the 318 trees bored in this study, the repeat releases registered by most of the older trees, the extent of the surrounding matrix stands, and the frequency of documented fires (Pickford et al. 1980) argue that only fire as a repeatable disturbance could have contributed the growth releases we documented.

All fire event data in this study were derived from usable increment cores taken from 318 living Douglas-fir trees. We were most interested in Douglas-fir >300 yr old, because they presumably had survived and recorded the one or two high severity fires noted by Fonda and Bliss (1969). Because the size of the study area encompassed more than 25 km^2, topographic maps, aerial photos, and ground reconnaissance were used to identify candidate trees and groves. Groves containing older trees were easily identified, because the canopy of the forest appears rough and coarse-grained (Fig. 1). We identified matrix forest types that delimited the physical borders of different fire events, and worked with candidate trees within smaller groves. Trees >300 yr old, however, often occurred as single survivors in younger forest types. Even when groves of a few >300 yr old trees were located, their area was ~1-2 ha. Because we worked in a wilderness, access was an important consideration. All sites had to be within 5 hr cross-country travel from roads and trails in the study area. We targeted multi-layered, uneven-aged, older groves, because they had the best chance to contain the fire event data we sought. We also worked in single-layered, even-aged younger groves, many of which contained survivor trees. The younger trees in these groves lacked fire release markers, but we used their germination dates as evidence of fires near 1900.

We analyzed 15 cut saplings to determine the number of years required for trees to reach 1.4 m tall. We determined this value on naturally germinated saplings ~15-30 yr old growing in open, previously forested sites and on downed trees ~60-70 yr old that had grown in stands that had originated in the open. We dated the cut trees at the root collar and at 1.4 m. The mean age difference between the two markers was 11.7 ± 0.5 yr. The low standard error associated with this sample indicated that the 12 yr factor was accurate for our estimates, with a possible difference of ±1 yr from the germination dates we present. This 12 yr value was added to the pith age of each tree at 1.4 m to obtain a closer estimate of year of germination and stand establishment.

Mean FRI based on fire release markers was calculated for each individual tree core. The bulk of the data came from Douglas-fir >250 yr old. Trees with the longest record of fire history were invariably the oldest and largest trees, which had survived and recorded one to six fire events in their lifetimes. Survivor trees >250 yr old, growing in matrix types <150 yr old (Fig. 2), carried the best long-term evidence of fire events in this drainage. Survivor trees in separated groves often recorded separate fires. We also located trees >300 yr old in small groups of up to five trees, all of which had survived past fires. We built our FRI

database from 318 single-point samples into progressively larger units of land, working with the fire intervals represented by the trees specific to the unit of land in question. Documented 20th century wildfires in the eastern Olympics commonly burned small areas (Pickford et al. 1977), leading us to assume the same relationship for presettlement fires. Although our FRI data progress from point fire frequencies to area frequencies (Agee 1993), we intend to focus our discussion on ~200 ha units because that is the general area of the tributary drainages to Maiden Creek in the study area.

Although trees were bored in groves throughout the drainage, we selected 23 sites to characterize the matrix forest types. Data on tree species (density and diameter class) and understory species (percent cover) were gathered on one 16-m radius macroplot per selected site. We chose this size primarily because the area of groves comprising trees >300 yr old commonly was ~1000 m^2. Data for downed and dead fuel weights were gathered on six 15.3 m transects at each of these selected sites using the methods of Brown (1974). Fuels <2.54 cm diameter were tallied along 182 cm of line (10.9 m total length per site), fuels 2.55-7.62 cm diameter were tallied along 364 cm of line (21.8 m total length per site), and fuels >7.62 cm diameter were tallied along the full length of the line (91.8 m total per site). Mass of standing dead elevated fuels (>2 m above the top of the organic soil horizon) was calculated using density values obtained from the macroplots and an equation derived from commercial harvest weights for each species and size class. These values were combined for each plot for total standing dead mass.

The research was designed so that FRI among various sized units and fuel loads among forest types could be analyzed by completely randomized design ANOVA. Significant differences among the treatments were determined by Newman-Keuls multiple range test (Zar 1999). Significance level was set at 5% for all tests before the data were collected.

Results

Matrix forest types

Three matrix forest types were present in the Morse Creek drainage, among which age, composition, structure, and fire history differed. These types are named according to the age of the trees that form the matrix forest, so that the Douglas-fir 1 type (DF1) is <150 yr old, the DF2 type is 150-300 yr old, and the DF3 type is >300 yr old. In actuality, few stands in the study area were 150-200 yr old, so that the effective age range of the DF2 type is 200-300 yr. Every DF1 and DF2 matrix type contained a few trees much older than the given age limits. These older, large diameter trees survived the fire that destroyed the previous matrix stand, and occurred only as widely scattered individuals or in small groups, often near the limits of the fire (Fig. 2). Presumably, they were the parent trees of the postfire matrix forest.

The data in Table 1 speak to density and diameter class, and provide information on dominant and subordinate positions within the forest. Trees with smaller diameters formed a fragmented, intermediate layer below the canopy. Douglas-fir dominated all three matrix forest types, with the greatest density and basal area among all trees >14 cm diameter (Table 1). For DF1 and DF2 types, there were considerably more western hemlock than Douglas-fir <14 cm diameter. Only in the DF3 type were there more small Douglas-fir than western hemlock.

In the DF1 matrix type, shade tolerant western hemlock and western redcedar (*Thuja plicata*) were well represented in diameter classes <25 cm, but were virtually absent in the larger size classes. Standing dead stems were a mixture of Douglas-fir and western hemlock. A mean of 38% of the standing stems in the DF1 matrix type were dead. Although the DF1 type was the youngest of the three matrix types, Douglas-fir trees >64 cm diameter and >250 yr old always were present (Fig. 2; Table 1). The understory was depauperate. Step moss (*Hylocomium splendens*) and Oregon beaked moss (*Kindbergia oregana*) combined for 25% cover. More than 12 herbaceous understory species grew in infrequent openings, but never attained 2% cover. Rocks and bare ground together accounted for 64% of the forest floor, and tree litter was a prominent component of the forest floor.

The DF2 matrix type was characterized by large Douglas-fir 200-300 yr old, with western hemlock and western redcedar well represented in the smaller diameter classes (Table 1). Trees >300 yr old, with records of past fire events, were

TABLE 1. Size class distribution (trees/ha) of the three matrix forest types in the study area. The DF1 type was <150 yr old, the DF2 type was 150-300 yr old, and the DF3 type was >300 yr old. The category "other species" includes all species present in small sizes and densities: western white pine (*Pinus monticola*), Pacific yew (*Taxus brevifolia*), red alder (*Alnus rubra*), Pacific silver fir (*Abies amabilis*), and subalpine fir (*A. lasiocarpa*).

Species	Diameter class (cm)								Total
	<3	3-13	14-25	26-38	39-51	52-64	65-76	>76	
DF1 matrix type									
Douglas-fir	–	384	471	105	74	25	1	21	1081
Western hemlock	–	1560	125	19	5	1	17	–	1727
Western redcedar	–	268	31	7	28	–	–	–	334
Other species	–	69	51	6	27	–	–	1	154
DF2 matrix type									
Douglas-fir	25	116	146	277	52	40	10	10	676
Western hemlock	99	178	7	17	22	–	–	–	323
Western redcedar	–	161	–	5	2	–	–	–	168
Other species	–	29	12	–	–	–	–	–	41
DF3 matrix type									
Douglas-fir	113	507	267	103	62	23	11	11	1097
Western hemlock	128	366	219	142	28	–	–	–	883
Western redcedar	88	176	158	9	–	–	–	–	431
Other species	49	10	19	–	15	–	–	–	93

common in this type. Overall stand density was less than the DF1 type, as 51% of the standing trees were dead. The dead trees were mainly Douglas-fir and western hemlock from the smaller diameter classes, similar to mortality in the DF1 type.

Unlike the DF1 type, understory species were more common in the DF2 type. Step moss (48%) and Oregon beaked moss (9%) accounted for well over half of the understory cover. The DF2 type supported a strong shrub component. Salal (*Gaultheria shallon*) averaged 9% cover; red huckleberry (*Vaccinium parvifolium*), kinnikinnick (*Arctostaphylos uva-ursi*), and dull Oregongrape (*Berberis nervosa*) combined for another 10% cover. The only noteworthy herbaceous species was pipsissewa (*Chimaphila umbellata*), with 5% cover. Six other species averaged <2% cover each. Rocks and bare ground averaged 13% cover, and tree litter was abundant.

The DF3 matrix type had few dead standing trees, and a higher tree density of Douglas-fir and western hemlock than the DF2 type (Table 1). Although Douglas-fir was the dominant tree species, western hemlock and western redcedar accounted for many more 14-51 cm diameter stems than in the DF2 type. Large, evenly-spaced Douglas-firs that had survived numerous fire events formed an open crown layer. The older age classes of Douglas-fir and western hemlock had evidence of common pathogens and decreased vigor. The 620 Douglas-firs <13 cm diameter are an interesting characteristic of the DF3 types, because they address replacement potential for the future. These diameter class distributions indicate that populations of Douglas-fir in DF3 types are more stable than in DF1 and DF2 types.

The DF3 type had the best developed understory structure of the three stand types. Cover of step moss and Oregon beaked moss was 48%, but cover of the vascular species exceeded 70%. Salal (45%) and kinnikinnick (14%) dominated. Pipsissewa (4%), red huckleberry (3%), and dull Oregongrape (2%) were the other prominent species. Rocks and bare ground averaged <2% in the DF3 forests, and tree litter was less prominent than in the other two forest types.

Fire History

Wildfire is the common disturbance agent in the Morse Creek drainage. Wind, snow avalanches, and mass wasting can create small disturbances,

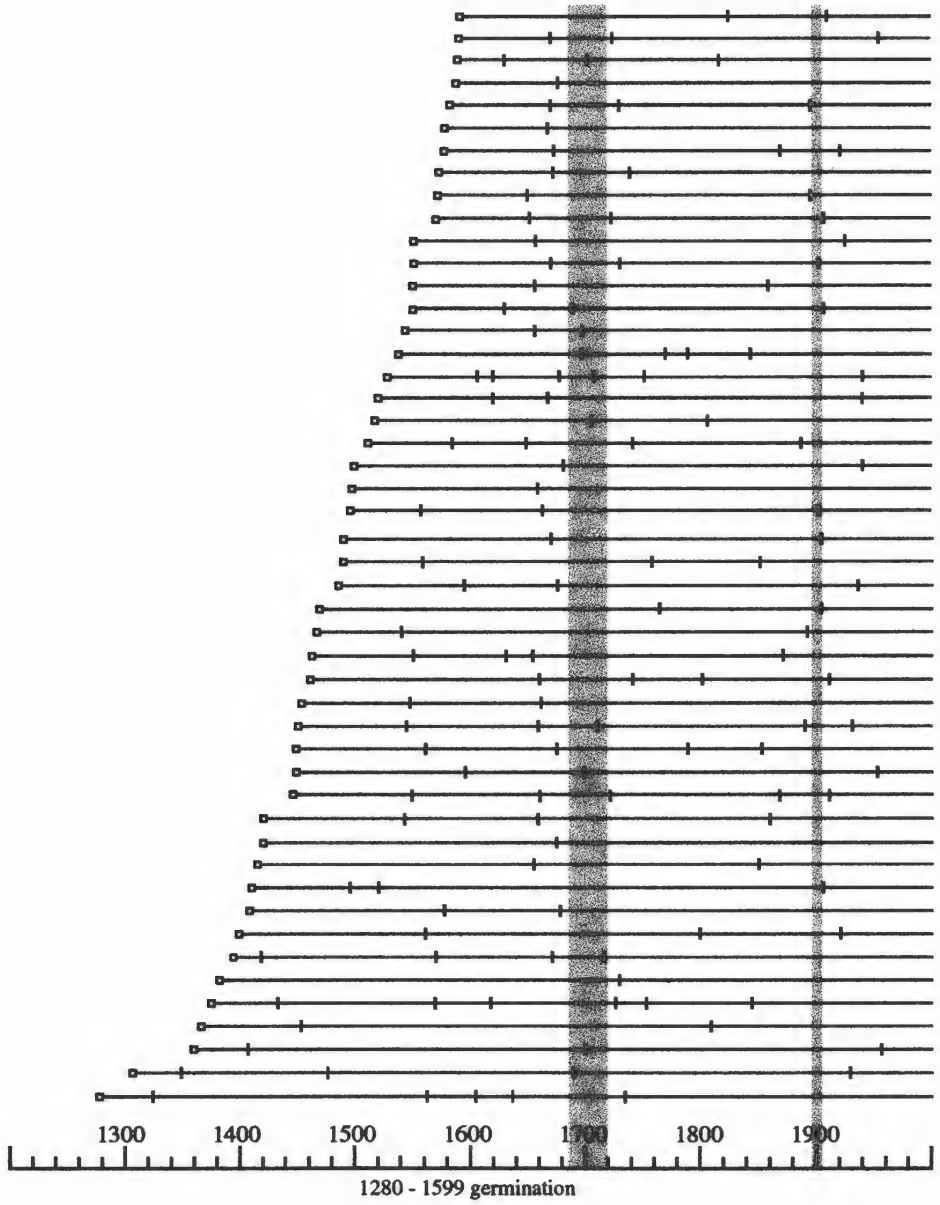

Figure 4. Fire records for trees that germinated before 1600. Germination dates are indicated by ❑, fire releases by ❙. The wide gray band marks the 1687-1720 burning period; the narrow gray band marks the 1897-1904 burning period. All trees were alive in 1994.

but these agents are infrequent and localized. The database of fire release markers and germination dates contains evidence of periods of widespread, high severity fires and smaller, low and moderate severity fires (Figs. 4-7). A series of fire years from 1687-1720 is indicated by the wide gray band

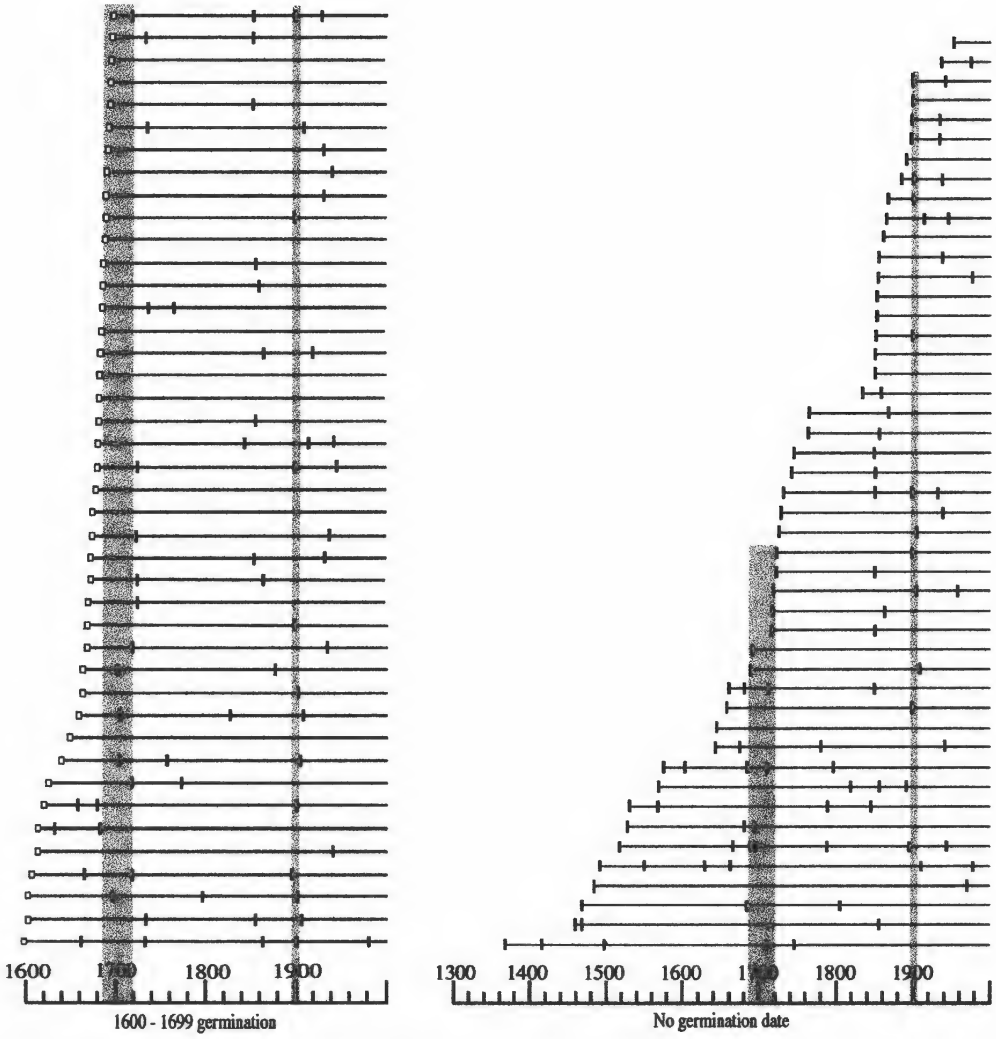

Figure 5. Fire records for trees that germinated 1600-1699 (left) and for trees with unknown germination dates (right). Germination dates are indicated by ❑. Lines for trees with unknown germination dates begin with the first fire event (❙). All trees were alive in 1994.

in Figures 4 and 5. The database contained 74 mature trees alive in 1700, of which 30 (41%) carried a fire release marker for 1687-1720. Germination in response to these fire years appears to extend from 1690 to 1740, when 59 of the trees in the database germinated (Fig 6). The trees that responded to this series of fire years now constitute the DF2 matrix type.

The narrow gray band in Figs. 4-7 marks a burning period from 1896-1904. The database contains 168 mature trees alive at this time, of which 43 (26%) carried a fire release marker for 1896-1904. Thousands of Douglas-firs in this drainage date from this burning period, and they form the DF1 matrix type. The forests formed by these trees are easily visible in the drainage (Fig. 1). Our

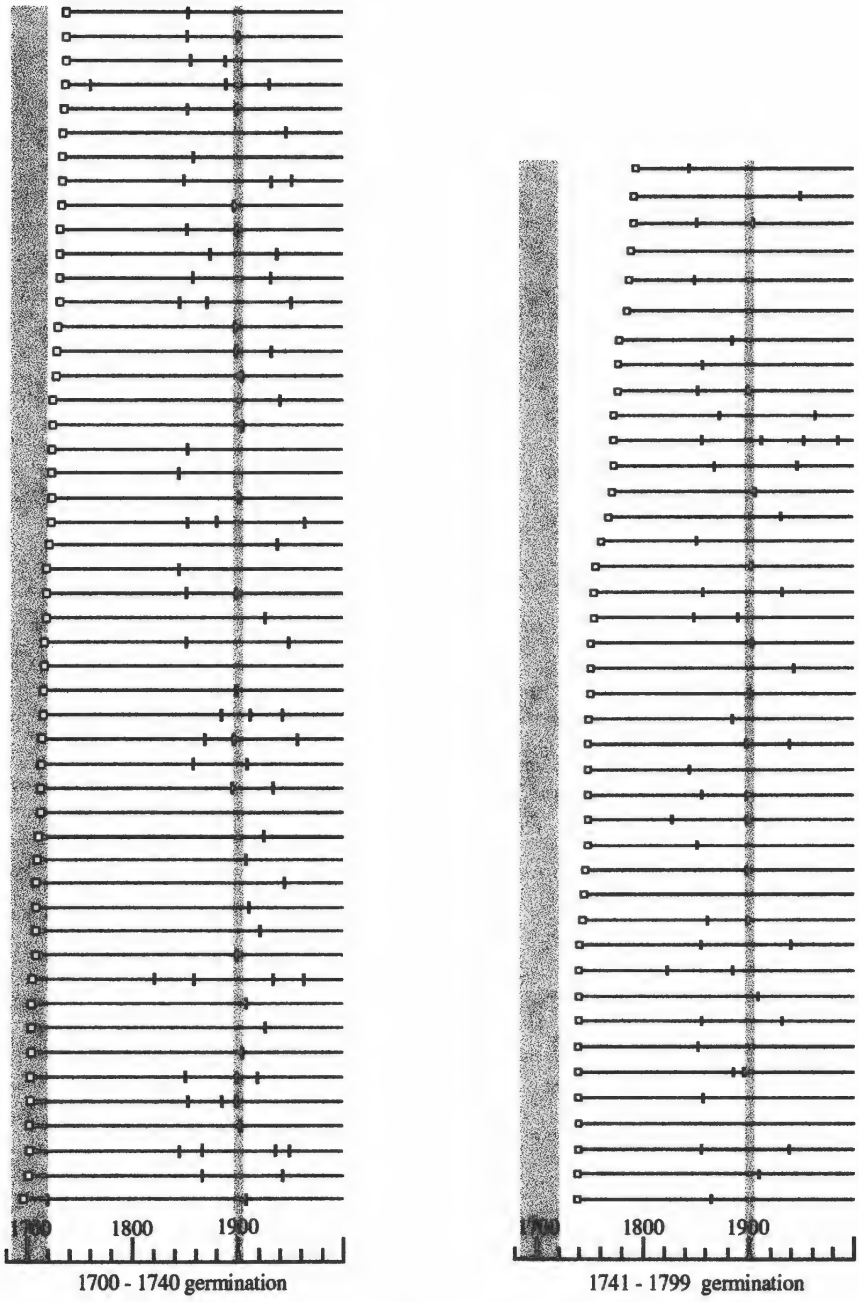

Figure 6. Fire records for trees that germinated 1700-1740 (left) and 1741-1799 (right). Germination dates are indicated by ❑, fire releases by ❙. The wide gray band marks the 1687-1720 burning period; the narrow gray band marks the 1897-1904 burning period. All trees were alive in 1994.

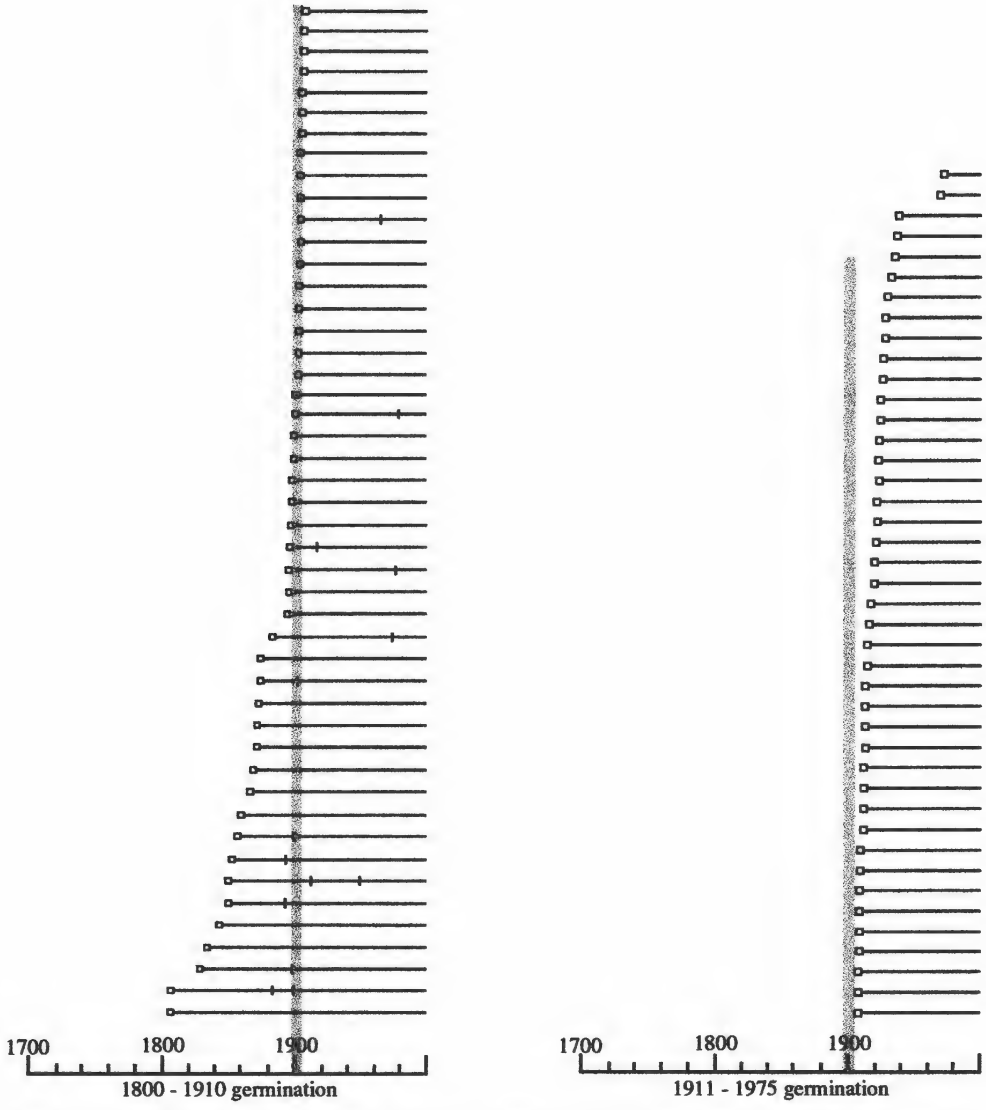

Figure 7. Fire records for trees that germinated 1800-1910 (left) and 1911-1975 (right). Germination dates are indicated by ❑, fire releases by ▮. The narrow gray band marks the 1897-1904 burning period. All trees were alive in 1994.

database contains 44 trees that germinated between 1898 and 1919 in response to these fires (Fig. 7).

The two major burning periods, during which widespread fires burned in the Morse Creek drainage, identified by the combination of fire release markers and germination dates have been known for many years. The forests that have developed in response to the two burning periods characterize the landscape in the Morse Creek drainage (Fig. 1). Additionally, many small fires were discovered in this research, and the evidence is not visually obvious across the landscape. Based on

fire release markers, unrelated fires burned throughout the drainage over the last 650 yr (Figs. 4-7). The earliest fire event recorded by release markers was in 1323, by a tree that germinated in 1280, the oldest tree in the sample (Fig. 4). Trees in the study area responded to the effects of a fire event on an individual basis. The variability among the release markers is high; few trees in the study area recorded the same fire event via growth releases. Only cohort trees in the same grove matched growth releases. Even then, differences of a few years remained in the actual record, depending on whether the growth increases came immediately after the fire, or after 1-2 yr of lower growth.

Decades during which at least 12 living trees recorded fire events by release markers are shown in Table 2. Few decades had <5 fires, and only during periods of above-average fire incidence did the number of recorded fires exceed 15. Some time periods were relatively free from fires, such as the early and mid-1600s (Fig. 8) and 1760-1840 (Table 2), whereas many trees recorded fire events 1841-1870 and 1880-1920 (Table 2, Fig. 8). There were, however, no decades when fire was completely nonexistent in the study area. Fires did burn somewhere in the drainage during each decade, even into the 1980s (Table 2, Figs. 4-8). The four decades from 1800 to 1839 had the fewest trees (12) with fire records, although other decades earlier than 1640 had fewer trees with recorded fires (Fig. 8). For example, fires were recorded by only seven trees during1580-1620. Data from pre-1640 must be interpreted with caution, however, because fewer trees alive then survived until 1994.

TABLE 2. Decades in which at least 12 trees recorded fires, by release markers only, in the Morse Creek drainage.

Decade	Number of fires
1670-1679	15
1710-1719	12
1720-1729	14
1840-1849	13
1850-1859	56
1860-1869	15
1880-1889	12
1890-1899	46
1900-1909	33
1910-1919	14
1930-1939	28
1940-1949	20

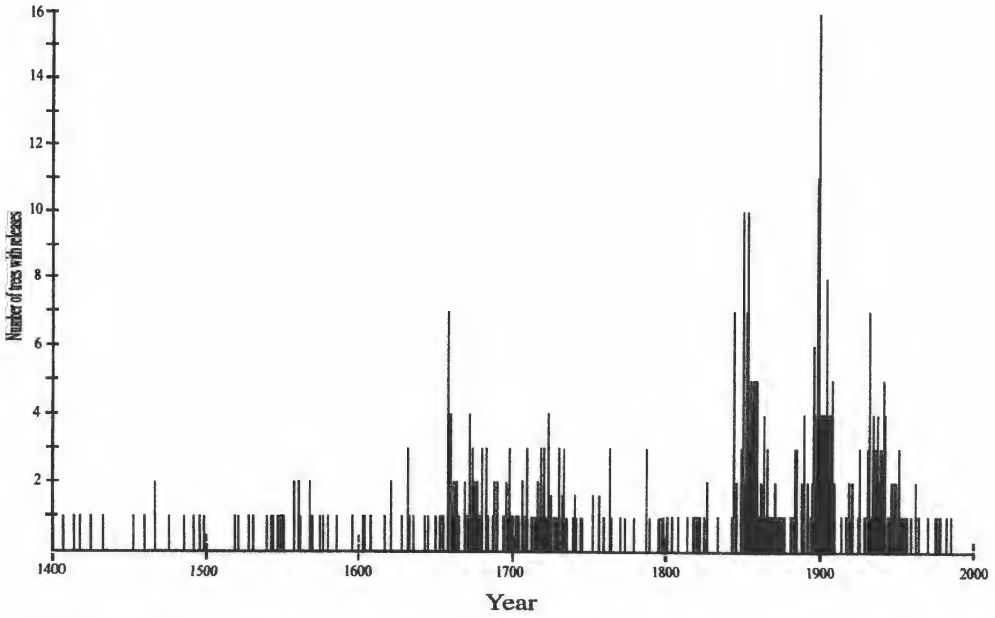

Figure 8. Number of living trees recording fire events 1400-1985.

Fire release markers from survivor trees in DF1 stands (Fig. 2) matched the ages of the younger trees in the postfire matrix stand (Figs. 4-8). Fire release markers were common in DF3 stands. Most trees >38 cm dbh had at least one release, and many 26-38 cm dbh trees also had fire release markers. Past fire events have favored shade-intolerant and fire resistant Douglas-fir over shade-tolerant, fire sensitive western hemlock and western redcedar.

Fire Return Intervals

Although we constructed separate FRI based on liberal and conservative growth criteria to reveal differences in tree responses to fire events, no significant FRI differences between liberal and conservative databases emerged for any landscape unit. We choose to present the liberal estimates, however, because we are convinced that definite fire events were excluded using the conservative criteria.

We calculated mean FRI at four spatial scales in the study area (Table 3). As the size of the unit increased, intervals between fires decreased. Tributary drainages in mountains are important fire ecology features, because wildfires often are confined by the ridges separating adjacent tributaries. Mean area for the lateral tributaries in the study area is ~200 ha, a size we believe yielded the most appropriate estimate of fire intervals in the forests of the Morse Creek drainage. At this spatial scale, mean FRI was 21 yr, with a median of 15 yr (Table 3). Of the 12 tributaries in which we gathered data, mean FRI for all but three was 11-22 yr. Two tributaries exceeded 40 yr. A confidence interval constructed from these data shows that the true mean FRI value on the tributary spatial scale lies between 13 and 30 yr, with a 5% probability of error.

Many groves on smaller units of land were distributed throughout the study area. Of the groves studied, 38 contributed to the mean FRI calculation. Each had at least three trees that carried multiple fire release markers, except for one grove in which two trees combined for seven fire release markers. Mean FRI for these 38 groves was about twice as long as the tributary level, and the median was about 17 yr longer (Table 3). Of the 38 groves, 20 had mean FRI between 20 and 40 yr, and fire returned to three of the groves on average <20 yr. All but two groves had mean FRI <100 yr.

TABLE 3. Fire return intervals (FRI) on four landscape unit sizes in the Morse Creek drainage, based on liberal criteria for growth release markers (Fig. 3).

Unit	Size (ha)	FRI ± SE (yr)	Median (yr)
One tree	<0.001	105.5 ± 6.1	91
Grove	0.1 - 1	44.3 ± 4.8	32
Tributary	200	21.3 ± 3.7	15
Morse Creek	2500	2.9 ± 0.3	–

Of the 318 Douglas-firs contributing to this study, 142 had multiple fire release markers, from which we could calculate FRI on the individual level (point frequency). Mean FRI was 106 yr, with a median of 91 yr (Table 3). Of the 142 trees, 37 had mean FRI of 50 yr or less, 80 had FRI <100 yr, 14 had FRI >200 yr, three of which had FRI >300 yr.

The entire drainage experienced a fire event on the average of once every 3 yr (Table 3). Pre-1650 mean FRI was 5 yr, somewhat longer than the overall mean because of fewer trees in the database. The longest time span without fire between 1400 and 1650 was 10 yr. From 1650-1985, the longest fire free interval was 8 yr (1780-1788), and post-1940 it was 6 yr (1964-1970). The longest interval during which at least one fire burned per year in the Morse Creek drainage was 1849-1862. If a fire had burned in 1863, this interval would have extended to 1871.

Standard errors generally were small, and declined as unit size increased. Individual trees were the most variable unit; the entire drainage was the least variable. These low standard errors indicate that fire is a regular environmental factor for these forests. It is noteworthy that standard error for the point frequency of fire on individual trees is merely 6 yr. Fire has returned often to the Morse Creek drainage, and few trees live their entire lives without experiencing one or two fires.

Fuel Loading

Surface woody fuels were significantly lower in the DF3 matrix type, and there were no significant differences between the DF1 and DF2 types (Table 4). Percent fine fuels (0.1-2.54 cm diameter) in the surface woody fuel component differed significantly across all three matrix types. Fine fuels represented a significantly smaller percentage of the surface fuels in DF1, and a

TABLE 4. Woody fuel loads (tons/ha) in DF1, DF2, and DF3 stands in the Morse Creek drainage. Like superscripts indicate no significant difference between the stand types. Percent fine fuels (0.1-2.5 cm diameter) were transformed by arcsin before statistical analysis.

	DF1	DF2	DF3
Surface fuels	48.5[a]	50.2[a]	31.0[b]
Percent fine fuels	22[a]	45[b]	56[c]
Elevated fuels	9.1[a]	1.9[b]	8.3[a]
Total fuel load	57.6[a]	52.1[b]	39.3[c]

significantly higher percentage in DF3. Elevated fuel mass did not differ significantly between DF1 and DF3, and both had significantly greater elevated fuel mass than DF2. Total woody fuel load was significantly different among all three types. DF1 had significantly higher total woody fuels, and DF3 had significantly lower total woody fuels. These fuel categories relate to the ages of the matrix stand types. In the DF1 type, for which 38% of the standing stems were dead and many more had fallen to the ground, coarse (>2.54 cm diameter) woody debris accounted for >27 kg/ha of the fuel component. The DF2 type had fewer total standing dead stems, but many decades of branch and twig fall contributed to the heavy surface fuels and high percentage of fine fuels. Standing dead stems were common in the DF3 type, but <14 kg/ha of coarse woody fuels characterized the sparse surface fuel component.

Discussion

The Morse Creek drainage supported a fine-grain mosaic of three matrix forest types (Table 1, Fig. 1) that reflect a mixed fire regime. The DF1 matrix type originated after stand-replacement fires. The DF2 and DF3 matrix types probably originated after high severity fires, but for the past three to five centuries have experienced only low to moderate severity surface fires. Any DF2 or DF3 units that had experienced high severity fires have been replaced by the postfire DF1 type.

The differences in woody fuels relate to the structural characteristics of the matrix types and to fire history. The younger DF1 type included small, standing dead trees, which contributed high amounts of elevated fuels. Abundant woody litter on the ground provides the fuel continuity to sustain fire and lift it to the canopy. The significantly lower percentage of fine fuels, however, argues that surface fires would be difficult to start and sustain to the point of igniting the large woody fuel loads. Thus, the DF1 type is unlikely to sustain low severity surface fires, but it could sustain high severity fires during extreme fire weather. Pickford et al. (1980) noted that the probability of crown fire was higher in these young stands. This relationship is reflected in the fire release data. Few trees that germinated in response to the 1896-1904 burning period carried fire release markers (Fig. 7).

The DF2 matrix type could support low, moderate, or high severity fires, depending on fire weather. Fires are more likely to be supported once ignited by lightning in this forest type. The significantly lower mass of elevated fuels argues that stand-replacement fires in DF2 would burn most probably under extreme fire weather conditions, which was the case in the two major fire episodes in 1687-1720 and 1897-1904. When low and moderate severity surface fires burn in DF2, the gaps in the downed woody fuel bed must be bridged by dead salal leaves and live mosses, salal, and kinnikinnick. Fire release data (Figs. 4-6) indicate that such low and moderate severity fires have started many times in the past in DF2, but low fuel continuity limited the spread to small areas. These fires probably were intense enough to kill western hemlock and western redcedar, leading to the growth releases in Douglas-fir.

The DF3 matrix type is likely to support low and moderate severity surface fires, largely because of the significantly lighter total fuel load. Although elevated fuel mass was significantly higher than in DF2, the lower surface fuel loads, coupled with higher densities of less-flammable western hemlock and western redcedar, argue against fires running into the canopy and developing into stand-replacement fires.

At any spatial scale from individual tree to the entire drainage (Table 3), all FRI estimates were shorter than FRI previously estimated for the eastern Olympic Mountains (Fonda and Bliss 1969, Fonda 1979, Henderson et al. 1989). Fires in the study area have burned more frequently and with more variable severity than the earlier 130-300 yr estimates. The fire regime is characterized by periods of 50-70 low and moderate severity fires, interrupted by infrequent, large-scale, high severity burning episodes (Figs. 4-8).

Based on date of stand establishment, Fonda (1979) and Henderson et al. (1989) identified two widespread, major fire episodes that burned in the area ca. 300 and 500 yr ago. Henderson et al. (1989) estimated FRI of 130-259 yr in large (>200 ha) Douglas-fir stands of the eastern Olympics, and stated that stand-replacement fires were common. In contrast to the data of Henderson et al. (1989), mean FRI based on fire release markers in this study equaled 21 yr on the 200 ha level (Table 3). Our germination and fire release data yielded no conclusive evidence of high severity fires earlier than 1680.

Fire history has been studied in other Douglas-fir forests on the Pacific slope. Since 1990, it has become clear that Douglas-fir forests ranging from northern California (Brown et al. 1999), through the Klamath Mountains (Taylor and Skinner 1998), the central Oregon Cascades (Morrison and Swanson 1990, Wallin et al. 1996, Cissel et al. 1998), to the North Cascades in Washington (Agee et al. 1990) have supported combinations of frequent low and moderate severity fires, and infrequent, high severity fires. Now the eastern Olympics can be added to the list, and the estimated FRI for northern forests dominated by Douglas-fir can be shortened considerably. Even at the level of individual trees, mean FRI was only 106 yr. These studies ranging from California to Washington demonstrated that low severity fires, presumably started by lightning, burned more frequently than high severity fires. The longest FRI was 94-137 yr in the North Cascades (Agee et al. 1990); the shortest was 13-22 yr in the Klamath Mountains (Taylor and Skinner 1998). Douglas-fir forests at Point Reyes actually supported 7-9 yr FRI (Brown et al. 1999). Although many of the fires were attributed to Native American burning, the short FRI establishes that Douglas-fir forests are capable of supporting frequent, low severity fires.

Fires throughout western North America have been less frequent since 1900 because of fire exclusion and changing land use patterns (Fonda and Bliss, 1969; Habeck and Mutch, 1973; Arno, 1976; Madany and West, 1980; Swetnam and Dieterich, 1983, Morrison and Swanson 1990, Brown et al. 1999). In the Morse Creek study area, the number of trees recording fires changed from 168 between 1841-1900 to 125 from 1901 to 1960 (Table 3), a decrease of ~25%. Most of the documented fires in this region were small (Pickford et al. 1977). Of the 140 fires documented by Pickford et al. (1977) for the eastern montane zone between 1916 and 1975, 76% burned <1 ha. Only 6% burned >20 ha, and the two largest burned 348 ha in 1924 and 121 ha in 1930. Nevertheless, in contrast to almost all other western regions, fires continued to burn in the Morse Creek drainage throughout the 1900s to the present (Table 3, Fig. 9).

The Little Ice Age extended from ~1600 to 1850 (Peterson et al. 1999). The fire record from the Morse Creek drainage appears to reflect the end of the Little Ice Age (Table 2, Fig. 8). Fire incidence during the Little Ice Age was low, and only four decades had a dozen or more trees that recorded fire (Table 2). The marked increase in 1850-1859 in the number of trees carrying fire release scars (Table 2, Fig. 8) appears to signal the drier and warmer conditions when the Little Ice Age closed. Of the 56 trees that recorded fires from 1850 to 1859 (Table 2), 10 recorded fires in 1850. Of the 71 trees recording fires 1850-1869 (Table 2), 52% recorded fires 1850-1855. Clearly, a long period of low fire activity ended dramatically as post-Little Ice Age weather became drier and warmer. One possible consequence of global climate change is a higher incidence of wildfires (Lenihan et al. 1998), presumably because extreme fire weather could be more common under drier and warmer conditions. Fires in the Douglas-fir forests in this region are governed primarily by fire weather, rather than by fuels (Agee 1997). If the climate in the eastern Olympics changes toward drier and warmer, so that the incidence and length of fire weather increase, fire events could increase suddenly, similar to the end of the Little Ice Age.

The fire history of the Morse Creek drainage provides a framework within which recommendations for managing fire in Douglas-fir forests in the eastern Olympics can be suggested. Lighting-ignited wildfires continued to burn in this area during the 20th Century, and they should continue into the future. Given the previous scenario of high intensity, stand-replacement fires every two to three centuries when extreme fire weather coincided with sufficient fuel loadings (Fonda 1979, Henderson et al. 1989, Agee 1997), fire exclusion and suppression were reasonable fire management strategies. This scenario no longer accurately describes the fire regime, however. Low to moderate severity fires have been common in

the Morse Creek drainage, but they have been small, not widespread. Management fires that burn many small patches of forest each year would approach the kind of fire regime typical of these forests. Such fires would perpetuate DF2 and DF3 matrix forest types, rather than allowing the fire avoider western hemlock to dominate the forests in the absence of fire. Furthermore, such fires would reduce fuel loadings, so that extreme fire weather would be less likely to cause high intensity, stand-replacement fires.

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Fire History of White Fir Forests in the Coastal Mountains of Northwestern California

Abstract

Fire intervals are presented for white fir forests in the coastal mountains of northwestern California. Fire dates were derived from fire scars and tree establishment dates from 28 logged sampling sites spread across an area approximately 125 km by 30 km. Pre-suppression median fire intervals ranged from 12 to 161 years. The median fire interval for the pre-suppression period (27 years) was significantly shorter than for the suppression period (74 years). There were no significant differences in median fire intervals among vegetation series. There were also no significant regressions of median fire interval with distance from the ocean, latitude, or elevation. Most sampling sites were multi-aged and had experienced multiple surface fires. Some sites had experienced stand-replacing fires. Fire suppression has increased stand density, increased the density of shade tolerant tree species, and decreased the density of shade intolerant tree species.

Introduction

Fire history studies of California white fir (*Abies concolor* (Gordon & Glend.) Lindley *var. lowiana* (Gordon) Andr. Murray) indicate that low elevation sites have shorter mean fire intervals than high elevation sites (McNeil and Zobel 1980, Agee 1991). Low elevation sites have been found to have mean fire intervals between 9 and 25 years (Kilgore and Taylor 1979, McNeil and Zobel 1980, Bork 1985) and on high elevation sites mean fire intervals have been determined to be 40 to 64 years (McNeil and Zobel 1980, Agee 1991, Taylor and Halpern 1991). These differences have been attributed to the cooler and moister environments that are often present at higher elevations (Agee 1993). Previous studies of white fir fire history have been conducted in inland locations. Little is known of white fir fire history in the coastal mountains of northwestern California.

Pre-European settlement fire ignitions were thought to be a result of both Native American fires and lightning (Agee 1993). Native Americans burned regularly in the vicinity of white fir forests on the Six Rivers National Forest to maintain plants used in basketry and for food and clothing (Heffner 1984, Blackburn and Anderson 1993).

The objectives of this paper are to: 1) report fire intervals for white fir forests in the coastal mountains of northwestern California and to compare them with other fire history studies of California white fir, 2) compare fire intervals among the different vegetation series containing white fir in the study area, 3) investigate whether elevation, latitude, or distance from the Pacific Ocean are associated with median fire intervals in these stands, and 4) infer the role fire and fire suppression have had on species composition and stand structure.

Study Area

This study was conducted within the Mad River and Orleans Ranger Districts on the Six Rivers National Forest. Study sites were located on a series of mountain ridges that separate the Six Rivers National Forest from the Klamath and Shasta-Trinity National Forests. In particular, sites were located on South Fork Mountain on the Mad River Ranger District and on ridges above Bluff Creek on the Orleans Ranger District (Figure 1). Sampling sites were found on all aspects and at elevations from 1,183 m to 1,646 m. The most southerly sampling sites were 127 km from the most northerly ones, and the most easterly sites were 31 km from the most westerly ones. The white fir forests on the Six Rivers National Forest are among the most westerly, occurring from 26 km to 81 km from the Pacific Ocean.

Annual precipitation varies from 175 cm on South Fork Mountain to 230 cm on the ridges above Bluff Creek (Miles and Roath 1993). Ninety-four

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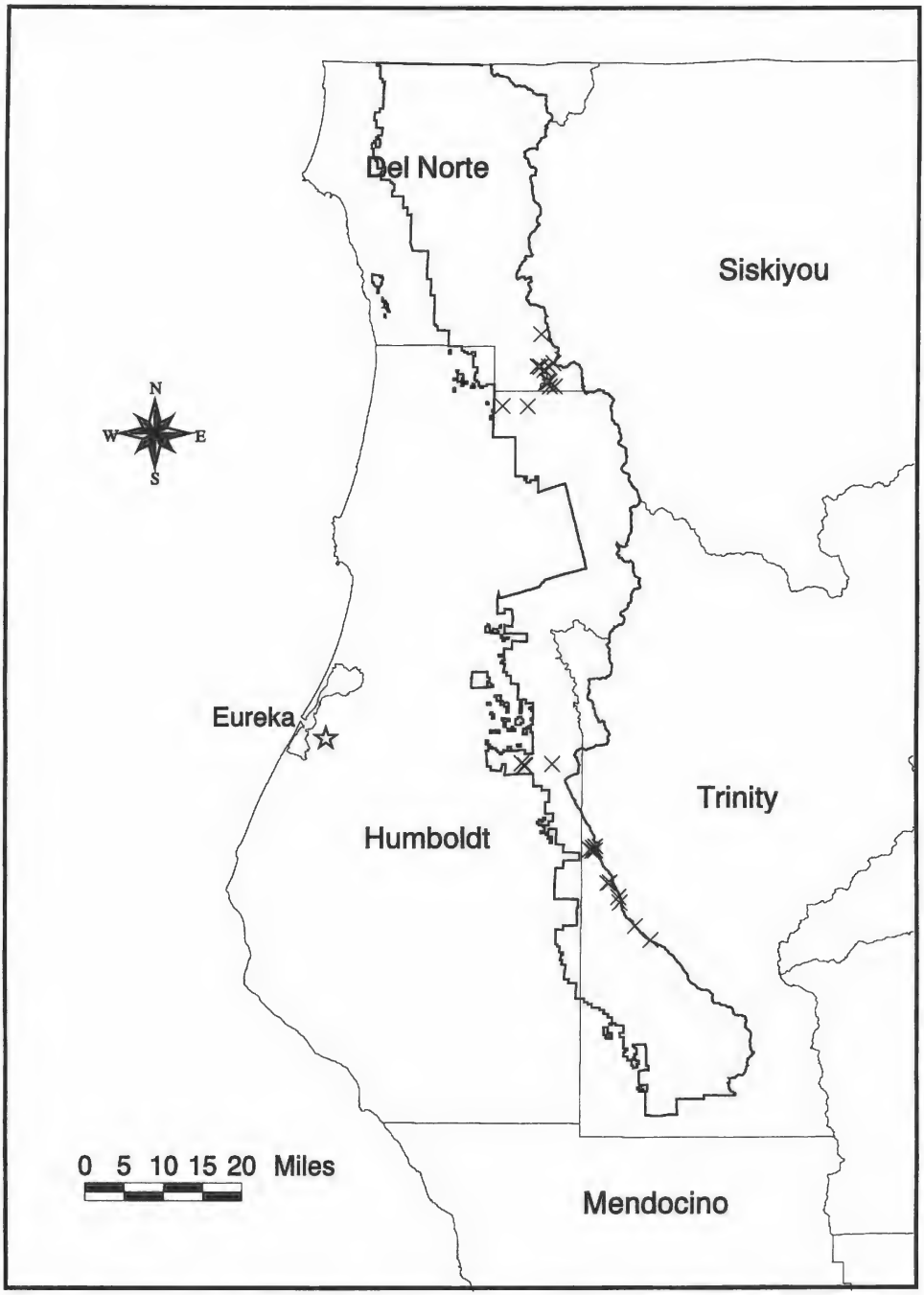

Figure 1. Location of sampling sites on the Six Rivers National Forest in northwestern California. Bolded lines are the national forest boundaries.

percent of the precipitation occurs during the months from October through May (Elford and McDonough 1964). Temperature and relative humidity are strongly moderated by the proximity of the Pacific Ocean. For a given elevation, winter temperatures are typically warmer and summer temperatures are cooler than more inland forests. The average July high temperature at Weitchpec, the closest weather station with similar weather to the study sites, is 28.6°C. The sampling sites, being at higher elevations, would be 5° to 8° cooler (Elford and McDonough 1964). In mid-summer, relative humidity averages 40 to 50% (Elford and McDonough 1964). East winds can dramatically reduce relative humidity and increase temperatures. During a 3-year period in Eureka, winds blew from the east 5% of the time, from the northeast 6% of the time, and from the southeast 17% of the time (Elford and McDonough 1964). Thunderstorms accompanied by lightning occasionally occur, but less often than in the Klamath Mountains, Cascades, or the Sierra Nevada (Automated lightning detection system April 1985-November 1997).

Study sites were located in forests with white fir either occurring as the dominant or co-dominant species. Other associated conifers included Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), incense-cedar (*Calocedrus decurrens* (Torrey) Florin), Port Orford-cedar (*Chamaecyparis lawsoniana* A. Murray), noble fir (*Abies procera* Rehder), and sugar pine (*Pinus lambertiana* Douglas). We classified each sampling site as belonging to one of three possible vegetation series: White fir, Douglas-fir, and Incense-cedar (Sawyer and Keeler-Wolf 1995).

Fire suppression records date to 1910 on the Six Rivers National Forest. Aggressive fire suppression and prevention of Native American and miner ignited fires in remote areas on the Six Rivers National Forest, however, did not begin until the end of World War II. Other studies from the Klamath Region found that fire frequency decreased in the 1940's (Agee 1991, Wills and Stuart 1994, Taylor and Skinner 1998), presumably because of more effective suppression efforts.

Methods

Twenty-eight sampling sites were located in logged areas that were dominated or co-dominated by white fir. Sampling sites ranged in size from 1.2 to 10.9 ha, with a mean size of 4.2 ha (s.d.=2.4 ha). The sampling sites were chosen to be coincident with logged areas to take advantage of readily available stumps. The sites, therefore, were not located without bias and may not reflect the variation found throughout the range of white fir in the broadly defined study area. We chose this sampling scheme because it was easier to find fire scars on stumps than on trees. Most trees in our area, as well as in other similar vegetation types in the Klamath Mountain region (Taylor 1993, Wills and Stuart 1994), have completely healed over fire wounds due to long fire-free intervals. Trees that did have open fire wounds were almost always rotten. Stumps from recently logged sites, in contrast, yielded good, sound wood.

Stem cross-sections were removed from all sound stumps having visible fire scars and were cut as close to the ground as possible, usually within 30 cm. Cross-sections were prepared with a power sander and sanded with successively finer grits of sandpaper whenever necessary to render an easily readable surface. Once prepared, the cross-sections were aged using a hand lens, and in some cases, a binocular microscope. Annual ring counts were made on one or more radii, depending on growth and ease of interpretability. Fire scar dates were recorded as well as tree age at the time of logging. Fire scars were recognized using criteria described by McBride (1983). Some trees had no fire scars but were aged as they presumably represented a cohort having been established following fire. Three years were added to the ages of trees at the time of logging to derive tree establishment dates after a reconnaissance sample determined the mean age of stump-high seedlings. Cross dating of tree rings (Stokes and Smiley 1968) was not possible with most specimens, presumably because competition influenced radial growth more than climate. Other studies have also found cross dating to be difficult in northwestern California (Brown and Swetnam 1994, Wills and Stuart 1994, Taylor and Skinner 1998).

A master fire chronology for each sampling site was prepared based on fire scar dates and years of establishment of even-aged cohorts. Fire scar dates that were uncertain were either discarded or adjusted using the techniques described by Arno and Sneck (1977). Only confirmed fire dates were used to calculate fire interval statistics. The Kruskall-Wallis H-test was selected to be used to detect significant differences in median fire

intervals between vegetation series and historic periods after the data were proven to be non-normal. Simple linear regression was used to assess whether median fire intervals had a statistically significant linear relationship with elevation, latitude, or distance from the Pacific Ocean.

Succession inferences for white fir forests on the Six Rivers National Forest were derived using data from Talbert (1996). Talbert (1996) demonstrated stand density and species changes using data collected in 1961-1963 on U.S. Forest Service Continuous Forest Inventory plots and then remeasured in 1993-1995. He used stand density index as a standardized density measure. Stand density index is based on the number of trees per 0.4 ha for trees 25 cm in diameter at breast height and is independent of age and site quality (Reineke 1933, Stage 1968). We reanalyzed Talbert's data after selecting for forests containing white fir.

Results and Discussion

A total of 126 fire-scarred stumps was found in the sampling areas. The number of fire-scarred stumps per sampling site varied from 0 to 11 with a mean of 4.5. These stumps produced an aggregate of 238 aged fire scars and an average of 8.5 aged fire scars per sampling site. Tree establishment dates were used as surrogates for fire dates on sampling sites without fire-scarred stumps and on sites with evident cohorts of white fir. A total of 112 trees was used to represent cohorts across all sampling sites.

Median fire intervals for all sampled sites ranged from 12 to 161 years. Fire intervals were highly variable within sampling sites with coefficients of variation ranging from 21 to 114%. Pre-suppression median fire intervals (27 years) were significantly shorter than the suppression period (74 years) ($P<0.001$). Mean fire intervals, however, were longer for both the pre-suppression period (35 years) and the suppression period (83 years). The median and mean number of years since the last fire was 74 years and 78 years, respectively (Table 1). There were no significant differences in median fire intervals between vegetation series ($P=0.284$)(Table 2). There were also no significant regressions of median fire interval as functions of distance from the Pacific Ocean ($r^2=0.001$, $P=0.86$), latitude ($r^2=0.044$, $P=0.29$), or elevation ($r^2=0.052$, $P=0.25$).

TABLE 1. Fire intervals for the pre-suppression period, the suppression period, and since the last fire. Data are median fire intervals from the sampling sites. n = the number of sampling sites

	Pre-suppression period (1614–1944) (n = 26)	Suppression period (1945–1995) (n = 28)	Years since last fire (date of last fire: 1995) (n = 28)
Median	27	74	74
Mean	35	83	78
Standard deviation	30	34	39
Range	12-161	31-163	18-163

TABLE 2. Fire intervals (years) of vegetation series containing white fir. Data are median fire intervals from the sampling sites. n = the number of sampling sites within a vegetation series.

	White fir (n=16)	Douglas-fir (n=9)	Incense-cedar (n=3)
Median	40	26	16
Mean	49	31	45
Standard deviation	44	18	51
Range	12-82	16-161	15.5-104

The median and mean pre-suppression fire intervals (27 and 35 years, respectively) on our sampling sites were between fire intervals reported for inland low elevation and high elevation forests (9-25 years and 40-64 years, respectively) (McNeil and Zobel 1980, Agee 1991 Taylor and Halpern (1991). Our within and between site range in fire intervals are similar to those found in Douglas-fir dominated forests in the Klamath Mountains (Wills and Stuart 1994, Taylor and Skinner 1998), in Douglas-fir forests in the Cascades (Morrison and Swanson 1990), and in red fir forests in the southern Cascades (Taylor 1993). The somewhat longer fire intervals determined for our relatively low elevation sites are undoubtedly due to lower fire danger caused, in part, by the moist, cool climate of the Pacific Ocean. The summertime dome of cool, moist marine air usually extends to the first set of high ridges east of the ocean. East of these ridges, there are typically sharp summertime gradients of increasing high temperature and decreasing low relative humidity (Elford and McDonough 1964). Thunderstorms

and lightning are less frequent close to the coast than on inland sites (Elford and McDonough 1964, Automated lightning detection system April 1985-November 1997). Many fires, therefore, were probably ignited by Native Americans burning to culture basketry materials, food, and clothing (Heffner 1984, Blackburn and Anderson 1993).

Since the early 1960s, and presumably since fire suppression began, forests with white fir have become denser. Stand density indexes increased for all tree species combined, increased for tolerant tree species, and decreased for intolerant tree species (Table 3). Tolerant species were white fir, Douglas-fir, incense-cedar, and chinquapin (*Chrysolepis chrysophylla* (Hook.) Hjelmq). Intolerant species included California black oak (*Quercus kelloggii* Newb.), madrone (*Arbutus menziesii* Pursh), ponderosa pine (*Pinus ponderosa* Laws.), and sugar pine.

Changes in the proportional stand density index contributed by species over the sampling period revealed that white fir and chinquapin increased; incense-cedar contributed the same proportional amount to the overall stand density index; and Douglas-fir, ponderosa pine, sugar pine, Pacific madrone, and California black oak decreased (Table 3).

Most of the sampling sites were multi-aged and had experienced multiple surface fires. In most cases, there were more fire scar dates on a sampling site than there were cohorts of established trees. Most fires, presumably, were not severe enough to create sufficient growing space to reinitiate a cohort. Occasionally though, a surface fire was severe enough to allow tree re-establishment in gaps. On a few sampling sites there were dominant even-aged cohorts that presumably had become established following a stand replacing fire or wind event. These patterns are similar to those found in Douglas-fir/hardwood forests on the Klamath National Forest (Wills and Stuart 1994, Taylor and Skinner 1998), in mixed white fir forests in southern Oregon (Agee 1991), and in Douglas-fir forests from the central western Cascades of Oregon (Morrison and Swanson 1990). Fire has been the predominant stand replacing disturbance in these forests over the past several centuries and was presumably similarly predominant over the past few millennia.

TABLE 3. Thirty-two years of change in stand density indexes of major tree species occurring in white fir forests. Data are from Talbert (1996).

	1961-1963		1993-1995	
	Stand density index	Proportional stand density index	Stand density index	Proportional stand density index
all species	371.4	1.000	424.7	1.000
white fir	162.8	0.438	207.9	0.490
Douglas-fir	131.9	0.355	140.5	0.331
incense-cedar	14.9	0.040	16.8	0.040
chinquapin	2.3	0.006	2.9	0.007
California black oak	11.5	0.031	11.4	0.027
Pacific madrone	7.6	0.020	5.5	0.013
ponderosa pine	8.4	0.023	7.0	0.017
sugar pine	13.3	0.036	9.2	0.022
other species	18.7	0.050	23.5	0.055

Continued fire suppression in white fir forests on the Six Rivers National Forest should lead to further increases in total stand density, increases in stand density of tolerant species, and decreases in stand density of intolerant species. In particular, white fir should continue to increase in density and extend into previously unoccupied stands. The relative importance of Douglas-fir should continue to decrease relative to white fir in stands where they are co-dominant. Ponderosa pine, sugar pine, and California black oak should continue to decrease in density and will eventually be extirpated from more stands. These structural changes will increase live fuel loading and vertical fuel continuity.

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Avian Use of Recently Evolved Riparian Habitat on the Lower Snake River, Washington

Abstract

Since 1975 the U. S. Army Corps of Engineers has managed and irrigated 440 ha along the lower Snake River in Washington as mitigation for four dams constructed 1962-1975. We investigated avian use of irrigated Habitat Management Units (HMUs), compared to non-irrigated sites and streams that entered the river. We conducted bird surveys at 25 sites in summer and fall 1997 and in spring 1998. We compared avian abundance, species richness, and species diversity among habitats and seasons. We detected an average of 169 birds and 33 species at HMUs, 120 birds and 28 species at non-irrigated sites, and 63 birds and 23 species along streams in all three seasons. We detected an average of 29 species/site in summer, 31 in fall, and 22 in spring. Species diversity, as measured by the Shannon-Wiener function, was higher in summer, indicating that large flocks of a few species were common in fall and spring. These data demonstrated that the lower Snake River is an important stopover site for migrating birds. We detected an average of 30 more bird species than a study conducted on the same area in 1974. The increase in species richness is attributed to the development of HMUs and to natural succession of palustrine vegetation since dam construction. Future potential changes in reservoir levels, such as breaching of dams, will undoubtedly affect bird communities along the lower Snake River in all seasons. However, our data demonstrated that habitat perturbations can be partially mitigated by habitat enhancement and management.

Introduction

The importance of riparian zones for birds in the arid and semi-arid West has been well documented (Szaro 1980, Knopf and Samson 1988, Johnson 1989, Schulz and Leininger 1991, Douglas et al. 1992, Clary and Medin 1993). Western riparian zones generally have a higher structural and vegetative diversity than uplands. This leads to a higher number of niches and higher species density, richness, and diversity (Johnson 1989, Clary and Medin 1993). However, many western streams and rivers have been altered for hydropower production, resulting in the loss of riparian habitat (Lewke and Buss 1977).

Four dams were built on the lower Snake River between 1962-1975. These impoundments resulted in the loss of approximately 1,200 ha of riverine habitat (Corps 1991). In 1975, the U. S. Army Corps of Engineers (Corps) initiated the Lower Snake River Fish and Wildlife Compensation Plan to analyze and mitigate impacts to fish and wildlife resulting from these dams. The Corps acquired and/or designated 1,702 ha of land for wildlife habitat (Corps 1991). Approximately 440 ha have been developed as 10 intensively managed and irrigated Habitat Management Units (HMUs).

Several studies have been conducted to evaluate wildlife communities and habitats along the lower Snake River (e.g., Asherin and Claar 1976, Lewke and Buss 1977, Monda and Reichel 1989, Corps 1991, Downs et al. 1996); however, none have specifically addressed the wildlife value of irrigated HMUs. Our objectives were to estimate and compare avian abundance, species richness, and species diversity among irrigated HMUs, non-irrigated riparian sites, and streams that entered the river. These data were part of a report submitted to the U. S. Army Corps of Engineers (Rocklage and Ratti 1998).

Study Area

The lower Snake River study area extended 209 km from Ice Harbor Dam near Kennewick, Washington, upriver to the confluence of the Snake and Clearwater rivers at Clarkston, Washington. The study area included four reservoirs: Ice Harbor, Lower Monumental, Little Goose, and Lower Granite. See Asherin and Claar (1976) and Lewke and Buss (1977) for a detailed description of the study area.

Twenty-five study sites were selected for bird surveys in 1997 and 1998. Study sites were divided among three habitat types: 7 irrigated HMUs, 7 non-irrigated sites, and 11 streams. Irrigated

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HMUs were located on bars or benches along the Snake River and were intensively managed and irrigated. They were characterized by patches of trees and shrubs interspersed with upland habitats and crops planted for wildlife such as hay, corn, sunflower, and millet. Trees commonly planted on irrigated HMUs were Russian olive (*Elaeagnus angustifolia*), poplars (*Populus* species), dogwood (*Cornus* species) and black locust (*Robinia pseudo-acacia*). Shrubs included Siberian pea (*Caragana arborescens*), buffaloberry (*Shepherdia* species), rose (*Rosa* species), and Himalayan blackberry (*Rubus discolor*). Unmanaged upland habitat was largely composed of forbs and grasses, especially of cheatgrass (*Bromus tectorum*), bluebunch wheatgrass (*Agropyron spicatum*), and Sandberg bluegrass (*Poa sandbergii*). Rubber rabbitbrush (*Chrysothamnus nauseosus*) and big sagebrush (*Artemisia tridentata*) were also common in upland habitats. Shoreline habitat included white alder (*Alnus rhombifolia*), scrub-willow communities (*Salix* species), and palustrine-emergent vegetation, such as cattail (*Typha* species), bullrush (*Scirpus* species), and reed-canary grass (*Phalaris arundinacea*).

Non-irrigated sites were also located along the river. They typically had narrow strips of palustrine shrub-scrub and palustrine-emergent vegetation along the shore, which developed naturally since dam construction and subsequent formation of reservoirs (Downs et al. 1996). Palustrine vegetation was immediately bordered by upland vegetation.

Study streams or drainages entered the Snake River, and ranged in size from the relatively large Tucannon River to small, narrow canyons with ephemeral streams. All drainages had woody vegetation, although type and quantity of vegetation often varied dramatically depending on seasonal water supply, annual precipitation, and slope of canyon walls. Riparian vegetation was immediately bordered by upland vegetation. Most streams had white alder, but in various sizes and densities. Himalayan blackberry was also common. Palustrine willow and emergent vegetation often occurred along streams, particularly at the confluence with the Snake River.

Methods

We placed bird-survey stations 400 m apart along a transect at each site. On irrigated HMUs and non-irrigated sites, stations were located approximately equidistant between shoreline and inland edge of the bench. Stations along streams were placed on the edge of riparian vegetation. There were 44 stations on irrigated HMUs, 43 on non-irrigated sites, and 46 along streams.

The variable-circular plot (VCP) method (Reynolds et al. 1980) was used to survey birds. We surveyed birds in three seasons; summer (i.e., the breeding season), fall, and spring. Breeding-bird surveys took place from mid-May through mid-July 1997. Fall surveys occurred during September and October of 1997, and spring surveys from mid-March through April 1998. Each survey station was visited four times in summer and three times in fall and spring. Observers rotated among stations to distribute potential differences in observer ability. To distribute differences due to time of day, we also rotated the order stations were visited (Robbins 1981). Surveys began at or near official sunrise and continued until 1000. Surveys did not take place during rain or when wind interfered with observer's hearing ability.

Each VCP survey was 10 minutes. Observers recorded species of all individual birds detected and distance in meters to each bird. Birds that flushed as the observer approached the station were counted as if they were detected during the survey. All flocks and family groups were recorded as such. Birds or flocks flying over the sampling area were recorded separately because it could not be determined whether these birds were using the sampling area; however, birds that flew within sampling-area vegetation were recorded as detections within the VCP. Birds that flew from another area and landed in the sampling area after the survey began were recorded as flyovers.

Density estimates (birds/10 ha) for each site in each season were calculated with the ordered-distance method after Roeder et al. (1987). We chose this nonparametric method for its lower variance estimate and robust nature under a variety of situations (Roeder et al. 1987). The method calculated an effective survey area for each species. At least 30 detections of a species were needed to calculate a reliable effective area (Burnham et al. 1981). Given that one assumption of the method is that each detection is independent (Roeder et al. 1987), we calculated density of flocks if greater than 20% of a species detections were of flocks. Flyovers were not

included in density-estimate calculations. All detection distances were truncated to 200 m at each station to eliminate those outside the target habitats. Effective areas were calculated separately for each season since species' detectability may vary among seasons (Gutzwiller 1991). Because observer-hearing ability can change in different habitats (Schieck 1997), an effective area was calculated for each habitat type for those species with more than 30 detections in each type.

Swallows are difficult to accurately survey with the VCP method. Their swift, darting flight make it difficult to count and measure distances to all individuals. Furthermore, it is uncertain whether they classify as flyovers. Therefore, observers counted the number of individual swallows observed at the beginning of the survey. We calculated relative abundance of swallows (average number observed) for each site in each season.

Because fall birds are less vocal and more cryptic, we also used an area-search method in fall. This method is similar to "bird watching" in that the observer wanders through an area and records numbers of each species seen or heard during a specified time period (Ralph et al. 1993). Observers were instructed to pay particular attention to dense-riparian vegetation and fruiting plants at all sites and crops at irrigated HMUs. They were allowed to take as much time as needed to identify birds. The search period occurred between sunrise and noon. The area-search method was only used to obtain a more complete species list for each site.

Survey data were used to calculate species richness and diversity. Species richness was total number of species detected at each site in each season. Both VCP and area-search data were used for calculation of species richness in fall. We used average number of each species detected at each site to calculate diversity in each season. Diversity indices measure the number of species and evenness of species representation in a community. We chose the Shannon-Wiener Function (H') because it is sensitive to changes in rare species in the community.

Shannon-Wiener function:

$$H' = \sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

where p = proportion of each species in the total sample.

Its theoretical maximum is $\log_2(S)$, where S is maximum number of species in the community. However, in biological communities H' rarely exceeds 5.0 (Krebs 1989).

Variables were checked for univariate normality prior to analyses with probability and quantile plots. Many species had non-normal plots due to zero entries at some sites. Because the research question is multivariate, species densities could not be used in the analyses. Therefore, data were collapsed into overall avian abundance; i.e., the average number of birds detected at each site. Avian abundance, species richness, and species diversity met the normality assumption and were used as dependent variables in a multivariate analysis of variance (MANOVA). The main effects were habitat types (irrigated HMUs, non-irrigated sites, and streams), seasons (summer, fall, spring), and their interaction. We used univariate F-tests and canonical correlations to examine which dependent variables contributed to significant main effects. Fisher's LSD was then used for multiple comparisons within treatments.

Results

We detected 92 species during the breeding season on the lower Snake River. Including flyovers, the five most frequently detected species were bank swallow (*Riparia riparia*; n = 1,185), cliff swallow (*Hirundo pyrrhonota*; n = 1,078), red-winged blackbird (*Agelaius phoeniceus*; n = 881), western meadowlark (*Sturnella neglecta*; n = 573), and Bullock's oriole (*Icterus bullockii*; n = 489). Absolute densities were calculated for 30 species. Red-winged blackbird (13.81 birds/10 ha), Bullock's oriole (10.63 birds/10 ha), American goldfinch (*Carduelis tristis*; 7.72 birds/10 ha), brown-headed cowbird (*Molothrus ater*; 7.81 birds/10 ha), and American robin (*Turdus migratorius*; 5.63 birds/10 ha) had the highest densities. See Rocklage and Ratti (1998) for additional results.

During fall 114 species were detected using both VCP and area-search methods. Including flyovers, the most frequently detected species were red-winged blackbird (n = 1,906), white-crowned sparrow (*Zonotrichia leucophrys*; n = 1,635), American goldfinch (n = 832), Canada goose (*Branta canadensis*; n = 742), and European starling (*Sturnus vulgaris*; n = 737). Starlings, however, were only abundant at one irrigated HMU.

Seventeen species had a sufficient number of detections to calculate density, and we calculated density of flocks for 11 of these species. White-crowned sparrow (17.69 flocks/10 ha, mean flock size = 5.10), song sparrow (*Melospiza melodia*; 14.50 flocks/10 ha, mean flock size = 1.32), savannah sparrow (*Passerculus sandwichensis*; 6.29 flocks/10 ha, mean flock size = 2.31), yellow-rumped warbler (*Dendroica coronata*; 2.30 flocks/10 ha, mean flock size = 3.20), and American goldfinch (3.22 flocks/10 ha, mean flock size = 2.56) had the highest densities.

We detected 91 species during spring. The most frequently detected species were white-crowned sparrow (n = 1,344), American goldfinch (n = 862), red-winged blackbird (n = 809), western meadowlark (n = 802), and Canada goose (n = 407). Of the 21 species for which density was calculated, white-crowned sparrow (4.28 flocks/10 ha, mean flock size = 5.86), song sparrow (6.90 birds/10 ha), western meadowlark (6.62 birds/10 ha), red-winged blackbird (5.30 birds/10 ha), and American robin (4.62 birds/10 ha) had the highest estimates.

There was no significant interaction between habitats and seasons in the MANOVA model (F = 0.772; df = 12,169; P=0.679); thus, the interaction term was removed. Main effects of habitat types (F = 5.744; df = 6,136; $P \leq 0.001$) and seasons (F = 8.574; df = 6,136; $P \leq 0.001$) were significant. Univariate F tests and canonical correlations showed that avian abundance (F = 24.685; df = 2,70; $P \leq 0.001$) and species richness (F = 14.206; df = 2,70; $P \leq 0.001$) were different among habitat types in all three seasons. Mean avian abundance was higher at irrigated HMUs (168.84 ± 22.91 birds) than both non-irrigated sites (120.47 ± 10.30 birds) and streams (62.55 ± 5.54 birds) (Table 1). Species richness showed the same trend, with more species found at irrigated HMUs (33.14 ± 1.52 species), followed by non-irrigated sites (27.91 ± 1.64 species) and streams (23.18 ± 1.48 species) (Table 1).

For the effect of seasons, species richness (F = 13.817; df = 2,70; $P \leq 0.001$) and diversity (F = 2.808; df = 2,70; P = 0.067) contributed to the significant MANOVA, and were different among seasons. Species richness was higher in fall (30.96 ± 1.84 species), followed by summer (29.32 ± 1.52 species), and spring (21.60 ± 1.31 species) (Table 2). Species diversity, however, was highest in summer (summer, Shannon-Wiener Function = 3.651 ± 0.157, spring = 3.291 ± 0.110, fall = 3.227 ± 0.133) (Table 2). Although the average number of birds detected was higher in fall, numbers were not statistically different. We detected

TABLE 1. Mean number of birds, number of species, and species diversity (Shannon-Wiener function) at irrigated Habitat Management Units (HMU), non-irrigated sites, and streams, lower Snake River, Washington, 1997-1998. Means combine summer, fall, and spring estimates. Different letters following means indicate significant differences (Fisher's LSD; $P \leq 0.100$).

				Irrigated HMU		Non-irrigated		Stream	
	F	df	P	Mean	SE	Mean	SE	Mean	SE
Number of Birds	24.685	2,70	≤ 0.001	168.837a	22.905	120.468b	10.302	62.545c	5.542
Number of Species	14.206	2,70	≤ 0.001	33.143a	1.517	27.905b	1.636	23.182c	1.483
Species Diversity	0.206	2,70	0.814	3.456a	0.163	3.406a	0.141	3.336a	0.122

TABLE 2. Mean number of birds, number of species, and species diversity (Shannon-Wiener function) in summer, fall, and spring, lower Snake River, Washington, 1997-1998. Means combine estimates from irrigated Habitat Management Units (HMU), non-irrigated sites, and streams. Different letters following means indicate significant differences (Fisher's LSD; $P \leq 0.100$).

				Summer		Fall		Spring	
	F	df	P	Mean	SE	Mean	SE	Mean	SE
Number of Birds	0.394	2,70	0.676	97.870a	9.075	121.880a	21.004	105.827a	14.429
Number of Species	13.817	2,70	≤ 0.001	29.320a	1.516	30.960a	1.843	21.600b	1.311
Species Diversity	2.808	2,70	0.067	3.651a	0.157	3.227b	0.133	3.291b	0.110

121.88 ± 21.00 birds in fall, 105.83 ± 14.43 birds in spring, and 97.87 ± 9.08 birds in summer (Table 2).

Discussion

Quality stopover sites that offer safe and plentiful food sources are critical for migrating birds (Moore et al. 1995). Such sites are probably most available in riparian areas in the arid and semiarid West (Moore et al. 1995). Our numbers indicated that all lower Snake River riparian habitats were important stopover areas during fall migration. Asherin and Claar (1976) observed more species on the lower Snake River in spring. Riparian habitats on the Umatilla National Wildlife Refuge along the Columbia River near Hermiston, Oregon, also appeared to have higher numbers of birds during fall migration than summer (S. Hudson, University of Idaho, Dept. of BioSci., Moscow, ID, pers. comm.). Because this was only a one-year study, we do not have data on annual variation in numbers or weather patterns. Unfortunately, we did not study avian communities along the lower Snake River during winter, and we feel this is an important area for future research.

Even though our methods detected more birds and species during fall, we feel that abundance estimates for fall were conservative for several reasons. First, bird song is decreased in fall; thus, we probably missed birds with the VCP method. Even though we detected more species with the area search (106 species with area search, 94 with VCP), this method was not standardized and abundances could not accurately be compared with those from the VCP. Second, 31% of all detections in fall were of flocks, compared to 20% in spring and 2% in summer. We believe there was often serious underestimation when counting birds in flocks, particularly when mixed flocks were foraging in dense-shrub patches. Species diversity was lowest in fall, which also indicated that large flocks of a few species, such as white-crowned sparrow and red-winged blackbird, were superabundant. Third, 18% of all detections in fall were of flyovers, compared to 11% in spring, and 7% in summer. Because it could not be accurately determined whether flyovers were using the survey area, flyovers were not included in any statistical tests. Birds that were flying over the area during surveys may have been using the Snake River corridor for migration. In addition, many flyovers were of large flocks that may have been disturbed by the observer. We therefore stress that our numbers may underestimate the value of the lower Snake River as a migration stopover site.

We demonstrated that more species and more birds were present at irrigated HMUs than at nonirrigated sites and streams in all three seasons. To further examine the importance of irrigated HMUs and other lower Snake River habitats, we compared our results with those from a study conducted in 1974 (Asherin and Claar 1976). They divided the lower Snake River into two reaches: Ice Harbor reservoir and from Lower Monumental dam to Clarkston, Washington. We divided our data similarly. In Ice Harbor, we detected 39 more species in summer, 49 more in fall, and 16 more in spring (Figure 1). In the second reach, we detected 24 more species in summer, 40 more in fall, and 14 more in spring (Figure 2). Although survey intensity differed and actual survey locations occasionally differed, we believe methodology alone cannot account for these dramatic differences. The increase in number of bird species detected likely was attributable to an increase in quality habitat since the first lower Snake dam was constructed in 1962 and the development of irrigated HMUs in 1975. In 1974 there was little or no shoreline vegetation, as previous vegetation was flooded and new vegetation had little time to develop. Monda and Reichel (1989) compared avian abundance and species richness along Lower Granite Reservoir pre- and post-impoundment. They found that riparian-associated passerines decreased from 1973 to 1981, and that upland-associated species correspondingly increased. This change was attributed to loss in riparian vegetation. A study conducted in 1996 showed an increase in palustrine emergent and palustrine shrub-scrub vegetation along the lower Snake River since 1987, particularly at slack water areas and at deltas of major tributaries (Downs et al. 1996). Therefore, birds have responded positively to habitats offered at HMUs and to the natural succession of riparian vegetation.

Future potential changes in reservoir levels, such as breaching of dams, will undoubtedly affect bird communities along the lower Snake River in all seasons. If the Snake River is allowed to return to pre-impoundment levels, effects on the avian community will be a complicated interaction among natural and management responses;

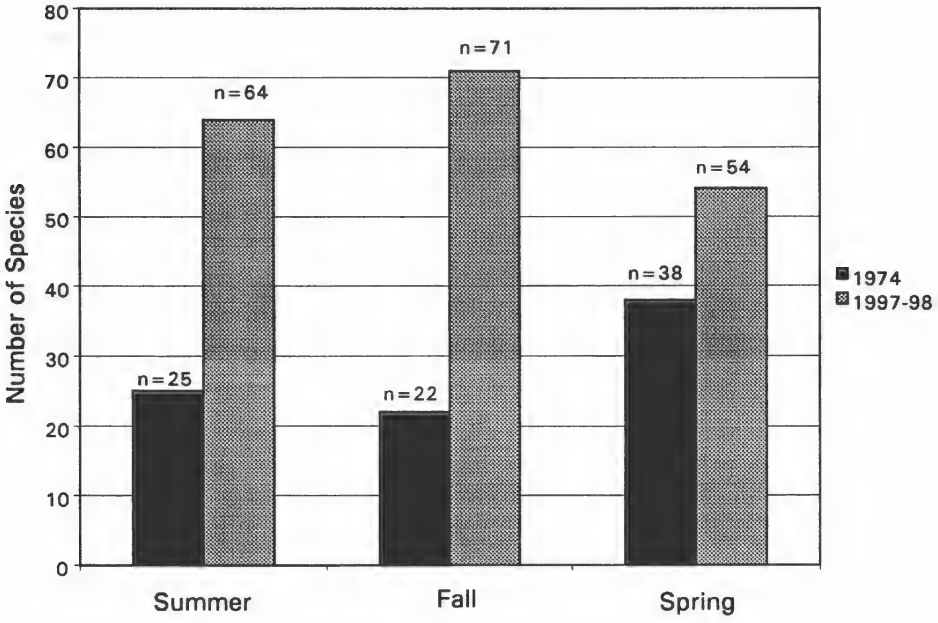

Figure 1. Number of bird species observed in three seasons along Ice Harbor Reservoir, Washington in 1974 (Asherin and Claar 1976) and in 1997-1998.

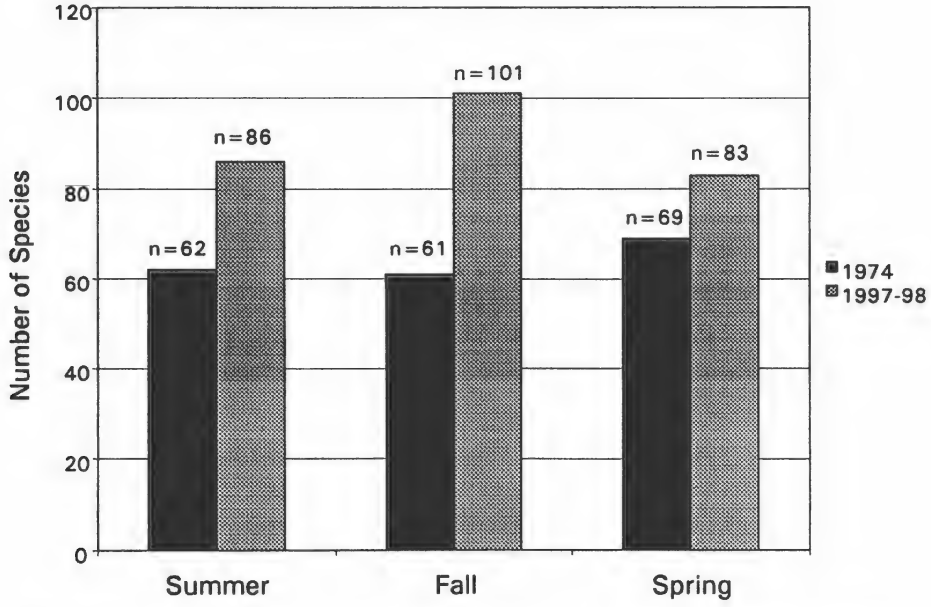

Figure 2. Number of bird species observed in three seasons from Lower Monumental Dam to Clarkston, Washington in 1974 (Asherin and Claar 1976) and in 1997-1998.

thus, predictions of changes in bird communities will be difficult. Current riparian vegetation may senesce as the water table drops. Upland vegetation will likely replace senescing riparian vegetation. Natural revegetation may take decades.

Breeding birds that may be immediately affected by lower water levels would be those that depend on willow shrub-scrub vegetation. Breeding birds, such as American goldfinch, Bullock's oriole, song sparrow, willow flycatcher (*Empidonax traillii*), yellow-breasted chat (*Icteria virens*), and yellow warbler (*Dendroica petechia*), may temporarily decrease in numbers (Monda and Reichel 1989, Knopf and Sedgwick 1992). Monda and Reichel (1989) noted a large decrease in numbers in American goldfinch and lazuli bunting (*Passerina amoena*) six years after construction of Lower Granite Dam. Although our data demonstrated that American goldfinch numbers have rebounded, lazuli buntings were still rare. Some birds will move into drainages, but drainages may be too small and narrow to support large numbers of nesting birds. Upland birds, however, may benefit from the gradual expansion of upland vegetation (Stauffer and Best 1980, Monda and Reichel 1989). Grasshopper sparrow (*Ammodramus savannarum*), horned lark (*Eremophila alpestris*), lark sparrow (*Chondestes grammacus*), ring-necked pheasant (*Phasianus colchicus*), and western meadowlark may increase on benches along the lower Snake River.

Migrating birds will also be affected by changes in water levels. Migrating birds need an adequate food supply and protective cover (Moore et al. 1995). These resources were readily available at irrigated HMUs, some non-irrigated sites and along larger streams during fall and spring. Migrating sparrows concentrated in weedy fields that offered a plentiful seed supply adjacent to protective cover, such as blackberry and willows (Strong and Bock 1990, A. Rocklage pers. obs.). Large flocks of red-winged blackbirds and sparrows were also observed in crop fields at irrigated HMUs during fall (A. Rocklage pers. obs.). Migrating white-crowned sparrows appeared to have benefited from the gradual expansion of riparian vegetation. Lewke and Buss (1977) detected 320 white-crowned sparrows prior to the construction of Lower Granite Dam, Monda and Reichel (1989) observed 14 six years after its construction, and our study detected 224. Along all four reservoirs, we estimated an average of 156 white-crowned sparrows per 10 ha at irrigated HMUs. This species has exhibited a significant population decline since 1966 in the western U.S. (DeGraaf and Rappole 1995); thus, Snake River habitats may be vital to current populations. Little is known about other quality stopover sites and migration patterns in the inland Northwest (Moore et al. 1995).

The comparison between our data and that from Asherin and Claar (1976) and Monda and Reichel (1989) clearly indicated that bird populations have rebounded from impoundment of the lower Snake River. This rebound was undoubtedly due to the development and management of irrigated HMUs, as well as to the natural succession of shoreline vegetation. However, we emphasize that it is unknown how annual variation, competition, predation, and cowbird parasitism affect bird populations on the lower Snake River. Our data demonstrated that future habitat perturbations can be partially mitigated by habitat enhancement and management.

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Reproduction, Growth, and Winter Habitat of Arctic Grayling in an Intermittent Canal

Abstract

Life history and winter habitat characteristics were determined for a population of Arctic grayling (*Thymallus arcticus*) in an irrigation canal with seasonally intermittent flow: (1) approximate locations and times of spawning; (2) growth rates; (3) numbers present in the residual pools and their survival through winter; and (4) depths and dissolved oxygen (DO) beneath ice cover of inhabited pools. Water flowed for five months from late April-early May to late September, peaking at 46-48 m^3/s and averaging 11.4°C (range 4.7-16.0). Reproduction within the upper canal was confirmed by sightings of spawning fish and observations and collections of developing embryos and newly swimming young. Spawning occurred in May, within one or two weeks after flow started. During the seven months without flow, 8 to 13 residual pools within the uppermost 6 km provided potential fish habitat. Four pools with combined length of 342 m and volume of 1487 m^3 provided the major wintering habitat during winter 1995-1996, and 76-100% of fish survived until spring in these pools. Under ice cover, mean DO ranged from 7.4 to 9.2 mg/l and mean depths from 0.26 to 0.82 m. These Arctic grayling had growth rates among the highest known among populations in Montana, but numbers of age-1 and older fish in the upper canal were estimated at less than 350 in spring 1995 and 1996. The persistence of this population, unlike their disappearance from all but one stream known to have been inhabited by the species in Montana, may be related to the failure of non-native fishes to become established in the canal, together with summer water volume and temperature and availability of wintering pools.

Introduction

Reports that a population of Arctic grayling was established in an intermittently-flowing irrigation canal were in sharp contrast to the disappearance of nearly all fluvial populations in Montana. Arctic grayling were historically widely distributed in the upper Missouri River and its tributaries above the Great Falls in Montana (Vincent 1962), but have disappeared from about 95% of that historic range (Kaya 1992). The only remaining fluvial population in Montana is confined to the upper Big Hole River. Although reasons for the decline of fluvial populations are not well understood, habitat alterations—especially construction of dams and dewatering of streams through diversions—and establishment of non-native salmonids appear to have been major contributing factors (Vincent 1962; Kaya 1992).

Arctic grayling have been present in Sunnyslope Canal since at least 1971, when fish were observed by Bill Hill (Montana Department of Fish, Wildlife and Parks, pers. comm.). The population apparently originated from repeated stockings of age-0 Arctic grayling into the canal's water source, Pishkun Reservoir, from 1937 to 1943 (Kaya 1990). These fish came from a state hatchery in Anaconda, and originated as gametes collected from an introduced population in Georgetown Lake. The species has not been caught in Pishkun Reservoir since 1981 (Bill Hill, pers. comm.), and is not established upstream in the Sun River drainage. Rainbow trout (*Oncorhynchus mykiss*), white sucker (*Catostomus commersoni*), and northern pike (*Esox lucius*) were also known to be present in the canal, possibly as fish being discharged out of the reservoir. Investigations into the life history and habitat characteristics of this population of Arctic grayling were conducted to determine conditions under which these fish have been able to persist in the canal.

Study Site

Sunnyslope Canal (Figure 1), constructed and managed to provide water for irrigation, is located in Teton County in west central Montana. Its source, Pishkun Reservoir, is at an elevation of 1341 m and receives water diverted from the Sun River.

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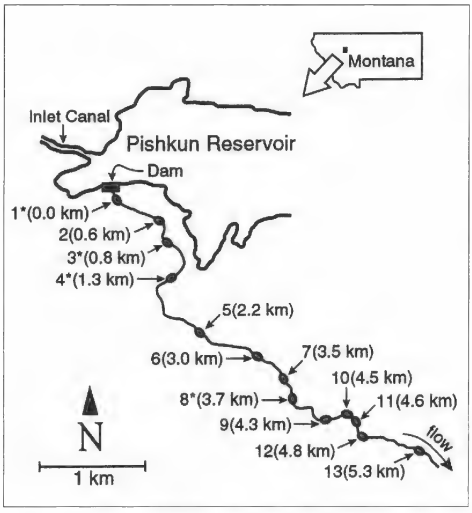

Figure 1. Locations of residual pools in upper Sunnyslope Canal when water is not flowing, numbered in downstream sequence. Distance from the canal's origin at Pishkun Reservoir is indicated by (km). Major wintering pools are identified by *. Lengths of pools are not to scale, and widths of pools are exaggerated to identify their locations. Actual pool widths are narrower than the canal.

The Sun River is a tributary of the upper Missouri River and originates in east slopes of the Rocky Mountains. Canal flow is controlled by the local Greenfield Irrigation District (GID), and is stopped for about seven months of the year. A steel screen at the dam (2.5 cm mesh) prevents larger fish from being discharged from the reservoir into the canal. The canal is from 24 to 32 m wide and from 2 to 3.5 m deep during peak flows. The canal has a sinuosity (canal length/straight-line-distance) of 1.2 and a gradient of 0.002% between the reservoir and the first drop structure 50 km downstream. The drop structures are concrete flumes angling steeply into plunge pools and are impassable barriers to upstream movements by fish. The canal is formed from rocks and soil of the regional glacial till, except for a 1.6 km concrete-lined section 9 km below the reservoir. The canal bed has a relatively smooth bottom and steeply sloping sides typical of an artificial ditch and lacks the habitat diversity of a natural stream. This study focused on the upper 6 km of the canal, where irregularities on the canal bottom retained residual pools of water after flow was terminated in the fall. The remainder of the canal goes dry before resumption of flows the following spring, except at the plunge pools below the drop structures.

Methods

Water Flow and Quality

Physical and chemical data were obtained during the periods of canal flow and from residual pools during non-flow periods, from April 1994 to April 1996. Data on daily discharge volumes were obtained from the irrigation district, which monitors a flow gauge near the dam. Surface temperatures were measured with a mercury thermometer. At two to three week intervals during the period of canal flow in 1995, dissolved oxygen (DO), pH, and alkalinity were measured with a field kit (Hach Chemical Company), and specific conductance with a YSI (Yellow Springs Instruments) Model 3000 conductivity meter. During fall 1995 residual pools were seined to determine which contained Arctic grayling (methods to be described). At least once monthly during winter 1995-1996, holes were drilled through ice cover over pools known to be inhabited by Arctic grayling, and specific conductance, DO (with a YSI Model 54 meter), ice thickness, and water depth beneath the ice were measured. Ice and water depths were measured with a weighted, calibrated line. On 8 March 1996 residual pool lengths, widths and depths were measured at 50 m intervals to estimate water volumes. The volume of each pool was estimated as [(length) x (maximum depth along the thalweg) x (0.5 average width)].

On 11 July 1995, water depths and velocities were measured at three locations known to be occupied by Arctic grayling, where numerous individuals could be seen feeding at the surface on drifting insects. Two locations were at km 0.8, about 50 m apart, and the third was at km 3.7 (Figure 1). At each site a calibrated line was secured across the canal and measurements were taken across the transect from a canoe, at 1 m intervals within 3 m of either bank and at 2 m intervals at other points across the transect. Velocities were measured with an electronic current meter (Montedoro-Whitney Company) with its sensor attached to a weighted, graduated cable. Measurements were taken at depths of 0.5 m intervals from the surface to the bottom.

Arctic Grayling Age, Size Distribution, Growth and Abundance

Fish were sampled primarily by seining, during March and April before canal flows began and again in September and October after canal flows ended. Fish were seined using a barricade net and a seine, each 30.5 m in length and with 6.3 mm mesh. A few Arctic grayling were also sampled by angling during canal flows. Total length of captured fish was measured to the nearest mm, and weight to the nearest gram. For length-frequency distributions, seined fish were separated into categories to the nearest cm. Age-1 and older fish were marked individually with a coded alphanumeric visible implant (VI) tag inserted into the clear tissue behind the eye (Haw et al. 1990). In 1994-95, VI-tagged individuals were also marked with fin clips so that fish could be identified as recaptures if VI-tags were not retained. Of 73 grayling recaptured from this group, 72 (99%) retained their VI-tags. Scale samples were taken from for age determinations from the area between the posterior edge of the dorsal fin and the lateral line (Jearld 1983). Ages were determined by analyzing impressions of scales on cellulose acetate slides, with the aid of a microfiche reader at 48X magnification (Jearld 1983). Lengths were back calculated using the Weisberg method (Weisberg and Frie 1987, Weisberg 1993a, 1993b). Assigned ages were verified by comparisons of independent readings by both authors, and also by recaptures of individually marked fish. Ages assigned by annuli and estimated lengths at annuli were verified by comparisons of changes in scale morphology vs. changes in body lengths indicated by length-frequency distributions and changes measured in 30 age-3 to age-7, individually marked, VI-tagged fish recaptured a year apart during spring samplings of 1994-1996.

Numbers of Arctic grayling present within the upper 6 km of canal that retained residual water were estimated during spring of 1995 and 1996. All 13 pools present were seined as were five deeper reaches between some of the pools. Other reaches between pools were very shallow, from a few cm to less than 0.5 m. Population abundance was estimated from mark and recapture data using Bayesian statistical procedures (Gazey and Staley 1986) incorporated into a computer program written by D. L. Gustafson (Montana State University, Environmental Statistics Group). Separate estimates were made for age 1 and for age 2 or older fish.

Winter Survival

Minimum survival through the winter in residual pools was estimated as the difference between numbers of fish marked in a pool prior to ice cover and number of marked fish recaptured during spring after ice cover melted but prior to canal flows. To provide an estimate of recapture efficiency and winter survival, 22 age-0 fish were moved from a drying pool below the study reach in fall 1995, VI-tagged, and added to the fish present in pool 8.

Spawning

Occurrence and time of spawning by Arctic grayling in the canal were investigated three ways: examining larger (300 mm or more) specimens captured during spring prior to water flow, sampling for age-0 young with drift nets, and visually surveying for the appearance of age-0 young along the canal margins. The gender of larger Arctic grayling was determined by the appearance and size of the dorsal fin, which is longer, higher, and more colorful on males than females. We subjectively evaluated whether females captured during spring prior to canal flow appeared to be carrying maturing eggs (abdomen distended) or were spent (abdomen soft and not distended).

Age-0 Arctic grayling were sampled with drift nets from early June to the end of the month. Nets were set at least three days per week, remained set for 24 hours each day and were examined at daybreak and nightfall. In 1994 three drift nets were placed at a bridge 5.8 km from the dam, and in 1995 two nets were placed at the bridge and two nets 100 m below the dam's outlet, on each side of the canal. At both dam and bridge, nets were suspended in the current at depths of about 1.0-1.5 m, within 1-2 m of the bank. The third net at the bridge in 1995 was suspended at midstream near the surface. Each net was 0.9 m in diameter, 1.5 m in length, had mesh size of 1 mm, and had a removable screened collection cup.

Visual searches for Arctic grayling fry were conducted from 4 June to 28 July 1994 and 1 June to 11 July 1995. Searches were focused on shallow, slower-moving water close to shore where newly swimming Arctic grayling in streams are typically present (Nelson 1954; Northcote 1995). Searches were concentrated within the uppermost

6 km of canal in both years, but also extended to 60 km in 1995. In 1995 the upper 60 km of canal was divided into five sections, 1 km subsections were randomly selected within each section, and three or four 100 m segments within each subsection were searched. Arctic grayling fry were identified by their size, shape, and swimming movements; their identities were confirmed by capturing samples with a dip net.

Other Species

Observations on other species were incidental and limited to specimens captured or seen during sampling for Arctic grayling. Specimens were identifiable as age-0 young from their initial appearances during canal flow and as they increased in size through summer and fall. Whether fish older than age-0 were adult in size was based on average growth rates and ages at maturation for the species in Montana (Brown 1971). The stomach contents of all captured northern pike larger than fry were examined to evaluate northern pike predation on Arctic grayling.

Results

Water Flow and Quality

Water was released from the reservoir into the canal from 6 May to 14 September in 1994 and from 22 April to 22 September in 1995. Flows peaked in both years at 46 to 48 m^3/s during June and early July (Figure 2). Flows were interrupted

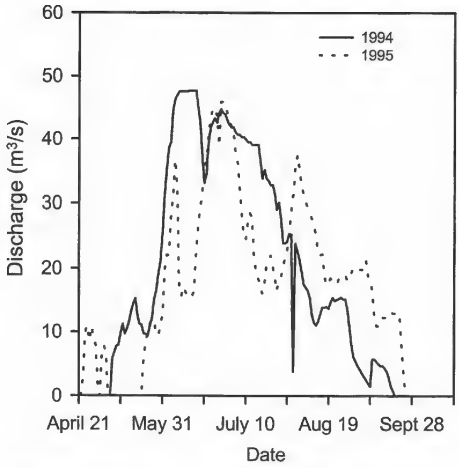

Figure 2. Discharge profiles for Sunnyslope Canal, 1994-95.

for 15 days in 1995, when discharge began on 22 April, stopped on 5 May when irrigation needs were suspended after heavy rainfalls, then started again on 20 May. During summer flows, Arctic grayling that subsequently overwintered in residual pools were captured by angling up to 9 km below the reservoir. Measurements on 11 July 1995 across three transects, at sites where numerous, larger Arctic grayling (numbers and sizes not determined) were observed feeding on surface insects, provide examples of depth and velocity profiles in the canal during summer flows (Figure 3). With canal flow of 28.5 m^3 the maximum

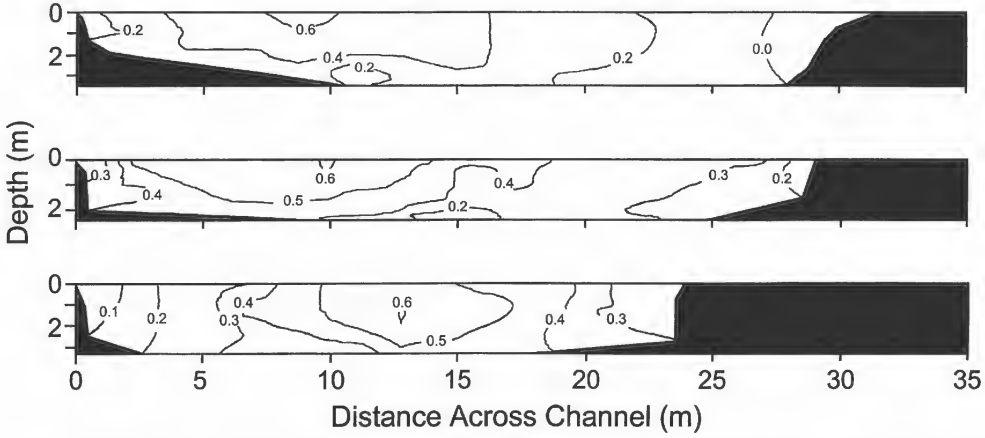

Figure 3. Velocity profiles (m/s) in the Sunnyslope Canal on 11 July 1995 across three transects through areas occupied by Arctic grayling. Canal flow on this date was 28.5 m^3/s. The upper two sites were about 50 m apart at km 0.8, and the lowest site was at km 3.7.

TABLE 1. Lengths and estimated volumes on 4 March 1996 of the 8 pools in upper Sunnyslope Canal which did not freeze to the bottom during the winter of 1995-1996, and numbers of Arctic grayling marked during fall 1995 and recaptured during spring 1996 in the pools.

Pool No.	Length (m)	Volume (m^3)	Number of Fish Marked in Fall	Number of Fish Recaptured in Spring	% Recaptured
1	217	160	25	19	(76.0)
2	93	50	0	0	(0.0)
3	146	244	9	8	(88.9)
4	250	263	33	30	(90.9)
5	213	198	0	0	(0.0)
6	64	113	0	0	(0.0)
7	88	167	0	0	(0.0)
8	700	980	7	7	(100.0)

TABLE 2. Mean and (range) of physical and chemical parameters during ice cover, of the four pools in Sunny Slope Canal known to be inhabited by Arctic grayling through the winter of 1995-1996: temperature (C), specific conductance (µmhos/cm), dissolved oxygen (DO, mg/l), ice thickness (cm), and water depth beneath ice cover (cm). Except for Pool 1, which had mean depth <0.5 m, chemical measurements presented were taken near the pool bottoms. Measurements taken at the tops of pools 3-8 near the ice surface generally had lower temperatures, higher DO, and lower specific conductance than near the bottom. Locations of pools are indicated on Figure 1.

Pool	Temp. C	Specific Conduct.	DO mg/l	Ice cm	Water cm
1	2.5 (1.1-3.3)	372 (366-380)	9.2 (8.2-11.0)	8.3 (0-15)	26.3 (11-40)
3	3.2 (1.9-4.5)	462 (275-425)	7.9 (6.5-8.2)	44.3 (30-58)	76.7 (70-90)
4	3.6 (3.0-4.1)	458 (447-470)	7.4 (6.5-8.2)	27.3 (20-35)	58.7 (50-63)
8	2.6 (0.7-4.1)	591 (450-786)	7.8 (4.7-9.1)	32.0 (32-38)	82.5 (80-90)

velocities were 0.5-0.6 m/s, and maximum depths 3.5 m. During the flow period of 1995, mean values for water quality measurements were: temperature 11.4°C (4.7-16.0), specific conductance 285 µmhos/cm (222-365), alkalinity 133 mg/l $CaCO_3$ (112-146), DO 12.2 mg/l (8.6-17.9), and pH 8.4 (8.0-8.5).

During the seven months (September to April) when water did not flow through the canal, up to 13 pools persisted within the uppermost 6 km closest to the dam (Figure 1). These residual pools received water leaking from the outlet gate at the dam, estimated by the irrigation district at less than 0.06 m^3/s, and probably from an unknown volume of discharge by springs within the canal bed. Pools were connected by narrow, shallow reaches of water from a few cm to about 0.5 m in depth, much of which froze to the bottom during winter. The pools had ice cover from November until early March in 1995 and early April in 1996. During the winter of 1995-1996, the five pools farthest downstream, pools 9 to 13, either froze to the bottom or became so shallow that surface ice contacted the bottom and then became overlain by water from snowmelt and rain.

Seining during fall 1995, prior to formation of ice cover, indicated Arctic grayling were present in four of the remaining eight pools—pools 1, 3, 4, and 8 (Table 1). During March 1996, toward the latter part of the annual period of ice cover, these four pools had a combined length of 342 m and volume of 1487 m^3 (Table 1). Characteristics of these four pools are summarized in Table 2 for winter 1995-1996. Dissolved oxygen remained

high in the pools, with averages ranging from 7.4 to 9.2 mg/l, and the lowest measured value of 4.7 mg/l. Mean ice thickness ranged from 8.3 to 44.3 cm, with the greatest measurement of 58 cm. Mean water depths beneath ice cover ranged from 26.3 to 82.5 cm, with greatest measurement of 90 cm.

Arctic Grayling Age, Size Distribution, Growth and Abundance

Arctic grayling attained a mean length of 158 mm at the first annulus and 302 at the second (Table 3). Growth rates estimated from annuli corresponded closely with sizes at ages indicated by length-frequency distributions (Figure 4). Males grew faster than females; by the fourth annulus males were significantly longer than females (t-test, $p = 0.03$), averaging 410 mm ($n = 11$, $SD = 13$), whereas females averaged 396 mm ($n = 10$, $SD = 15$). Comparison of body lengths of 11 VI-tagged Arctic grayling that were repeatedly captured during fall and spring 1994, 1995, and 1996 indicate that most growth occurred during the spring and summer period of canal flows (Table 4).

Estimated population sizes during spring 1995 and 1996 suggest that less than 350 Arctic grayling one year or older were present in the canal during the springs of 1995 and 1996 (Table 5).

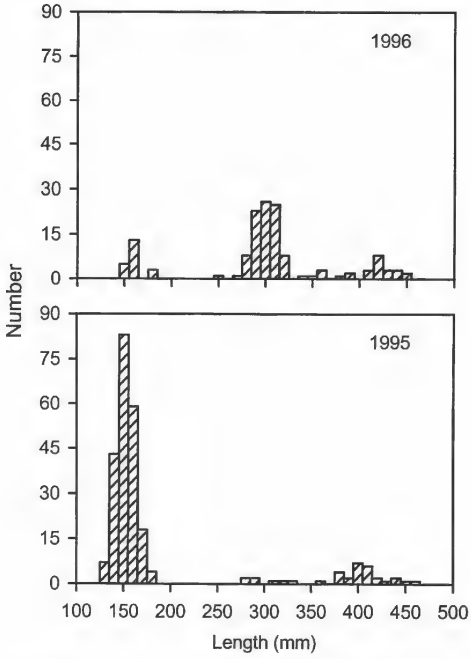

Figure 4. Length-frequency distributions of Arctic grayling in upper Sunnyslope Canal, in spring 1995 and 1996.

TABLE 3. Mean total length (standard deviation in parenthesis) and weight at time of capture and calculated mean total length at each annulus for Arctic grayling age 1 and older captured in Sunnyslope Canal in 1994, 1995, and 1996. N_W is the number of known-age fish weighed and N_L is the number of known-age fish measured.

Age Group	N_W	Mean total weight (g)	N_L	Mean total length (mm)	Calculated length (mm) at age						
					1	2	3	4	5	6	7
1	52	33 (9)	52	160 (12)	159						
2	59	252 (47)	62	301 (14)	161	301					
3	32	401 (61)	32	362 (11)	158	309	364				
4	18	564 (62)	21	403 (15)	151	299	361	407			
5	17	750 (127)	18	433	158 (16)	297	357	402	433		
6	3	758 (69)	4	437	155 (16)	298	357	398	429	425	
7	2	885 (261)	2	445	157 (7)	295	354	397	427	421	436
Mean back-calculated length (mm)					158	302	361	404	432	423	436
Mean increment of back-calculated length (mm)					158	144	59	43	28	-9	13

TABLE 4. Comparison of summer and winter growth (mm) for 11 recaptured, VI-tagged Sunnyslope Canal Arctic grayling, 1994-96. W94 = winter of 1994-95; S95 = summer of 1995; W95 = winter of 1995-96.

		Length (mm)									
	Age at	Fall	Spring	Fall	Spring	Growth Increments			Mean Increment		
Sex	First Capture	1994	1995	1995	1996	W94	S95	W95	W94	S95	W95
F	1	315	335	384	390	20	49	6	20	49	6
F	2	356	365	409	411	9	44	2			
F	2	—	280	349	349	—	69	0	9	57	1
F	3	406	405	436	442	-1	31	6			
F	3	392	384	420	425	-8	36	5	-4.5	33.5	5.5
M	4	—	417	429	430	—	12	1			
F	4	—	408	422	424	—	14	2			
M	4	—	402	429	420	—	27	-9			
M	4	—	409	428	425	—	19	-3	—	18	-2.3
F	5	—	408	418	415	—	10	-3	—	10	-3.0
F	6	—	442	446	450	—	4	4	—	4	4

TABLE 5. Population estimates for Sunnyslope Canal, spring 1995 and 1996, where n_1= number marked on first capture occasion; n_2= total number caught on first recapture occasion; m= number of marked fish caught on first recapture occasion; Nmle= population estimate; N_o= minimum population number; Nhi= upper confidence limit; Nlow= lower confidence limit; and STD= standard deviation.

Year	Age	n_1	n_2	m	Nmle	STD	N_o	Nlow	Nhi
S95	1	69	78	20	269	52.95	127	205	390
S95	2+	8	31	4	62	85.73	35	37	230
S96	1	19	15	11	25	4.18	23	23	36
S96	2+	77	105	67	120	3.54	115	116	129

Estimates are presented separately for age-1 fish and those two years or older (2+). Male:female ratios for fish age-2 or older were 1:2 in 1995 (n = 35) and 1:3.3 in 1996 (n = 107). Age-1 fish were much less common in 1996 than in 1995, suggesting poor spawning success during 1995 or low survival of the young.

Winter Survival

Results from seining the residual pools before and after the period of ice cover indicated high survival of Arctic grayling through winter, ranging from 76.0 to 100% (Table 1). Additionally, all 22 age-0 fish moved to pool 8 during fall 1995 were recaptured there as age-1 fish the following spring 1996. Fish remained in the same pools through winter; all Arctic grayling recaptured during spring 1996 were present in the same pool in which they had been captured during the preceding fall 1995. Also, fish tended to return to the same residual pools in fall of 1995 that they had occupied in 1994. Among 21 Arctic grayling that had been marked during the fall 1994 and recaptured during fall 1995, 13 (61.9%) were recaptured in the same pools as in 1994. Although most Arctic grayling were captured in residual pools, 40 age-1 and 3 age-2 or older fish were captured in reaches between pools in spring 1995. However, all of these reaches were immediately adjacent to a residual pool, and none were captured in other reaches.

Spawning

Both sexes of Arctic grayling became sexually mature at age 2. Sexual dimorphism of the dorsal fin was evident in fish ≥ 300 mm in length, and three age-2 females dissected in May 1994 contained maturing ova.

Arctic grayling spawned in the canal from early to mid-May, about one or two weeks after canal

flows began. During the springs of 1994, 1995, and 1996, a total of 88 Arctic grayling (≥300 mm total length) were examined within two days before canal flow began. None had freely expressible ova or milt, but all females had abdominal distention suggesting maturing ova. In 1994 and 1996, age-0 Arctic grayling were first seen between 8-14 June. Water temperature in the canal was 9-10°C since initiation of flows on May 6, and time to hatching and first swimming at this temperature would be about three weeks (Kaya 1990; Northcote 1995). Spawning was thus estimated to have begun about the second and third weeks in May, one to two weeks after seasonal canal flow started. Turbidity and high, turbulent flows through the canal prevented visual observations of spawning sites or activity in 1994 and 1996.

The temporary interruption of canal flow during spring of 1995, described earlier, provided an opportunity to visually confirm occurrence, location and time of spawning in the canal. Small flow volume from leakage at the dam produced riffles between some of the pools, and spawning was observed in one riffle at km 1.1 on 17 and 18 May, at water temperature of 9.8-10.5°C. Five large males established territories within the 18-m long riffle and were seen spawning with at least 5 females. White suckers were also observed spawning, at the downstream end of the riffle. Measurements taken at 2 m increments along the length of the riffle indicated a mean depth of 24.1 cm (range 15-45), mean width of 71 cm (range 61-81), and mean velocity of 0.30 m/s (range 0.17-0.43). Substrate consisted predominantly of cobble (diameters 10-50 mm) and gravel (2-10 mm). The riffle was sampled on 20 May by dislodging substrate upstream from a dip net, and embryos of both Arctic grayling and white suckers, distinguishable by differing egg diameters, were collected. Arctic grayling embryos were in varying stages of development; the most advanced had pigmented eyes, which would occur in about 7 to 10 days at water temperature of about 10°C (Henshall 1907). Spawning was not seen in other riffles through the 6 km study reach during the 15 days of interrupted flow.

Visual surveys and drift netting also indicated that newly swimming Arctic grayling originated from spawnings in the upper reaches of the canal. During summer flows of all three years, Arctic grayling fry were most commonly seen in the upper reaches of the study section. On 15 and 22 June 1995, 14 of the 17 fry found were in 4 canal segments from 1.3-3.7 km below the reservoir. Also seen along the canal margins, collected, and identified were many fry of white sucker, and a few fry of yellow perch (*Perca flavescens*) and spottail shiner (*Notropis hudsonius*).

Drift nets had limited effectiveness in capturing fish fry in the canal; however, results were consistent with observations on spawning and on visual locations of young. During June 1994 and 1995, a total of 25 Arctic grayling fry were captured in drift nets at the 5.8 km bridge, but none were captured in drift nets set at the dam outlet in June 1995 (nets were not set at the outlet in 1994). Drift nets indicated a reservoir origin for northern pike and yellow perch fry, with 50 northern pike fry captured at the dam outlet in 1995 but only 1 at the bridge in 1994 and 7 in 1995. Large, uncounted numbers of yellow perch fry were also captured in drift nets at the dam outlet and the bridge.

Other Species

Other species collected by seining in the upper canal were northern pike, rainbow trout, white sucker, spottail shiner, yellow perch, and mottled sculpin (*Cottus bairdi*). White sucker and mottled sculpin were common at sizes ranging from age-0 to adults. Northern pike and yellow perch were present mostly as age-0 fish, with only 14 northern pike and 1 yellow perch older than age-0 fish collected through the two years of sampling. No Arctic grayling were found among the stomach contents of the 185 northern pike whose stomachs were examined. Forty-two rainbow trout were collected in the canal, mostly older than age-0. Spottail shiners were collected in the canal only near the dam.

Discussion

Our results confirm that there is a small, self-sustaining population of Arctic grayling which grow rapidly in upper Sunnyslope Canal, despite extreme changes in habitat volume and characteristics. Estimated numbers of age-1 and older fish, averaging 238 during spring 1995 and 1996, represent densities of 26/km and 9/hectare in the upper 9 km of the canal during the summer flow period. These densities are lower than the 35/km and 28/hectare of age-1 and older fish estimated

for the upper Big Hole River (Liknes and Gould 1987), which supports the only riverine population of Arctic grayling in Montana, and much lower than densities of about 400 to 500/km reported for certain Alaskan streams (Oswood et al. 1992). During the five months of spring and summer flows, the canal appears to provide favorable conditions for growth of Arctic grayling. Growth rates of Arctic grayling in the canal are similar to those of adfluvial populations in Montana with rapid growths, Upper Red Rock Lake and Hyalite Reservoir, and exceed that of the fluvial population in the Big Hole River of Montana (Figure 5).

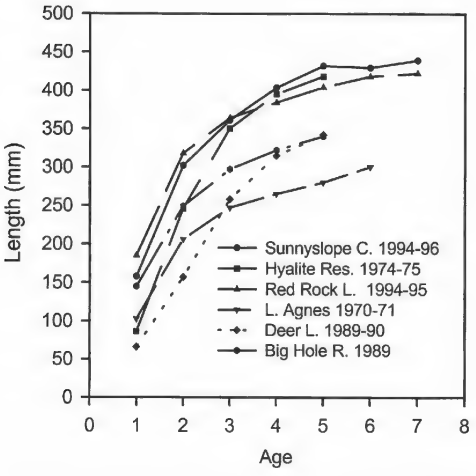

Figure 5. Growth curves of Arctic grayling in Sunnyslope Canal and examples of other populations in Montana: Upper Red Rock Lake (Mogen 1996), Hyalite Reservoir (Wells 1976), Lake Agnes (Peterman 1972), Deer Lake (Deleray 1991) and the Big Hole River (Shepard and Oswald 1989). Growth rates of Arctic grayling in Upper Red Rock Lake and Hyalite Reservoir are among the fastest known among populations in Montana (Kaya 1990, Mogen 1996).

Characteristics of the canal during both flow and non-flow periods may contribute to the ability of this population to persist there despite the disappearance of the species from most of the streams historically occupied in Montana. Peak flows greater than 45 m^3/s are similar to late summer flows of rivers in Montana which once supported Arctic grayling populations, including the Madison and Beaverhead rivers (U. S. Geological Survey 1983), and exceed summer flows of the Big Hole River. During midsummer flows, with a gradient of 0.002%, maximum thalweg velocities of about 0.6 m/s, and depth of about 3 m, the canal would resemble deeper reaches of a river with similar volume in a low gradient area. Historical accounts of Arctic grayling in the upper Missouri River basin (Evermann 1893; Vincent 1962) indicate that low-gradient reaches of the Missouri River and larger tributaries like the Madison River were important habitat for the species. During canal flow, temperatures remained cool and averaged 11.4°C, within the optimum range described by Hubert et al. (1985) for the species. Mean alkalinity (133 mg/l), pH (8.4) and specific conductance (285 µmhos) during summer flow in the canal were similar to values during summer for the upper Madison River in Yellowstone National Park (Zeikus and Brock 1972), and the upper Missouri River below its origin at its Three Forks (U.S. Geological Survey 1983), which were among the most important habitats for native fluvial populations of Arctic grayling in the upper Missouri River drainage (Vincent 1962).

Although availability of habitat was drastically reduced during seven months when water did not flow through the canal, conditions within the small volume of residual water did allow high survival of Arctic grayling. Dewatering of streams by human diversions commonly occurs during summer, when diminished flows not only reduce habitat space but also contribute to elevated temperatures that can reach lethal levels for Arctic grayling (Lohr et al. 1996). However, dewatering of the Sunnyslope Canal occurs from early autumn through mid-spring, when cooler temperatures prevail. By late winter in March 1996, the pools that provided the major winter habitat for the Arctic grayling were reduced to 1487 m^3 beneath ice cover. This would be the approximate equivalent of water volume present within only 16.5 m of canal length (with depth of about 3 m and width of 30 m) during peak summer flows, a volume reduction of over 99% from peak summer flows. The larger pools retained high concentrations of dissolved oxygen despite the shallow water that persisted beneath ice cover during the winter of 1995-1996. Estimated survival of Arctic grayling through winter ranged from 76 to 100%, at densities of about 0.2/m^3 (1023/ha), in the four known wintering pools during 1995-1996. Although survival rates and fish densities are not reported, a critical

role of wintering pools in frozen rivers has also been reported for Arctic grayling in Alaska (Reynolds 1989, West et al. 1992), and in the Big Hole River of Montana (Pat Byorth, Montana Department of Fish, Wildlife and Parks, pers. comm.). The drying out of most of the canal and use of residual pools for winter habitat could be considered analogous to the situation described for certain Alaska streams, in which stream reaches completely freeze and Arctic grayling occupy spring-fed pools during winter (Armstrong 1986).

Reviews of Arctic grayling reproduction in Alaska, Montana, and Canada (Armstrong 1986; Kaya 1990; Northcote 1995) indicate that different populations spawn at depths ranging from a few cm to more than 1 m, and over substrates ranging from silt to cobbles and boulders (unlike many other salmonids, Arctic grayling do not bury their eggs in excavated redds). The bed of Sunnyslope Canal is composed of varied substrates from fine sediments to cobbles, and water depth ranges from less than 1 m to more than 3 m as flow volumes change during the irrigation period. The spawning acts observed in 1995 occurred at shallow depths averaging only 24 cm and over coarse substrate, as has been described for some other populations (Kaya 1990; Northcote 1995). However, this activity occurred during an unusual set of circumstances when canal flow was temporarily stopped, except for leakage from the dam; a review of flow records indicated that this type of flow stoppage had not occurred during the previous 10 flow years (GID, unpublished data). Spawning also occurred during normal canal flows of 1994 and 1996, and the resident Arctic grayling thus appear able to spawn under widely varying flows and depths.

The inability of non-native species to become established in the canal may also be important to the persistence of Arctic grayling. Competition from or predation by non-native species may have been an important contributor to the decline of fluvial Arctic grayling in Montana; one or more species of non-native rainbow trout, brown trout (*Salmo trutta*) or brook trout (*Salvelinus fontinalis*) are established in all streams known to have been formerly inhabited by Arctic grayling (Vincent 1962; Kaya 1992). Although we did not observe northern pike predation of Arctic grayling, predation may still be important, especially in years when large numbers of northern pike are produced in the Pishkun Reservoir. Only white sucker and mottled sculpin appear to be maintaining populations in the canal, and among fishes present in the canal only these two species are native and sympatric with Arctic grayling in the upper Missouri River basin in Montana.

The other species in the canal appear to originate as small fish passing through the 2.5 cm outlet screen at the dam. Northern pike and yellow perch are known to spawn in the reservoir and small age-0 young were collected in drift nets below the dam. However, such age-0 young appeared to drift downstream with canal flow or followed receding water downstream when flows ceased, as few or none were present in residual pools during fall. Rainbow trout are established in the section of the Sun River from which water is diverted into the reservoir and are occasionally planted directly in the reservoir. Adult spottail shiners were visible in the reservoir at the dam and are small enough to pass through the outlet screen.

Although the population persists in the upper canal, many Arctic grayling, especially age-0 young, are lost downstream annually. After flows cease in September, hundreds of age-0 fish are present in temporary, drying pools farther downstream in the canal, in plunge pools at the bases of drop structures 50 or more km downstream, and in temporary pools in irrigation ditches which receive water from the canal (S. Barndt, unpublished data). We do not know whether these downstream losses occurred through summer or when water drained from the canal after outlet gates were closed at the dam. It is likely that such downstream losses have occurred throughout the existence of this population, and Arctic grayling ranging from age-0 to larger fish have been seen during fall at these downstream pools since at least 1971 (Bill Hill, pers. comm.). As has been proposed for other populations, such downstream losses may represent a continuing selective pressure toward the adaptation of a population to existence in upper reaches of a stream (Deleray and Kaya 1992).

Survival and reproduction of fish in the canal could be influenced by many factors. Physical factors could include effects of winter duration and severity on pool volume and water quality. Biological factors may include fish density per winter pool, and predation on age-0 grayling by other species transient in the canal, especially age-0 northern pike. Human activity also contributed directly to loss of Arctic grayling from the canal

during this study. The irrigation district removed and cleaned the screen surrounding the outlet at the dam in September 1994. For this operation the reservoir level was drawn down to about 0.5 m above the floor of the outlet tunnel and the outlet gate remained open. Age-0 Arctic grayling were visible in the shallow water of the outlet tunnel and its discharge area at the head of the canal, with many concentrated at and swimming against the outlet screen. We sampled and marked 782 age-0 fish in the tunnel and discharge area before the screen was removed but many more were present. To prevent loss of these grayling from the canal into the reservoir, the irrigation district constructed a low earthen barrier in the reservoir around the tunnel entrance. However, the barrier was breached by waves after the screen was removed and the age-0 fish disappeared, apparently lost into the reservoir. Thus, this population, confined seasonally to a few residual pools within only about 6 km of canal, may be very susceptible to influence from both natural factors and stochastic events related to canal operations.

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Canopy Light and the Distribution of Hemlock Dwarf Mistletoe (*Arceuthobium tsugense* [Rosendahl] G.N. Jones subsp. *tsugense*) Aerial Shoots in an Old-growth Douglas-fir/Western Hemlock Forest

Abstract

Hemispherical photography was used to quantify the relationship between canopy light and the distribution of hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) aerial shoots in an old-growth Douglas-fir/western hemlock forest to determine if aerial shoots only occur in higher light environments in the upper canopy. The Wind River Canopy Crane provided three-dimensional access by lowering a gondola into gaps between trees and stopping at 5 m intervals and sampling all trees around the gap at that height. A total of 89 dwarf mistletoe infections in live branches were sampled on 14 trees from 18 to 60 m. Forty-one infections had no aerial shoots whereas 48 had aerial shoots. All infections above 50 m had shoots, while all infections below 30 m (except one) had none. There were no aerial shoots at infections exposed to estimated insolation (yearly insolation = diffuse light * indirect site factor + direct light * direct site factor) of 1,000 MJ $m^{-2}yr^{-1}$, while all infections above 3,200 MJ $m^{-2}yr^{-1}$ had aerial shoots. Height and light were highly correlated but between 30 and 50 m the light environment became especially heterogeneous, with a 50% probability of aerial shoots occurring at 40 m, or at 2,200 MJ $m^{-2}yr^{-1}$. A complex of biotic and abiotic factors may account for the correlation of high light and aerial shoot occurrence in the field because laboratory studies have shown dwarf mistletoe produces the most aerial shoots in low light and high temperature. In this tall, multi-layered canopy, the source of the seed rain from western hemlock dwarf mistletoe was above the bulk of the western hemlock foliage, perhaps another explanation for the fast spread and intensification of mistletoe in old-growth forests.

Introduction

Dwarf mistletoes (*Arceuthobium* species, Viscaceae) are flowering plants that parasitize conifers, primarily members of the Pinaceae (Hawksworth and Wiens 1996). These perennial, dioecious parasites are endophytic within branches of the host tree. Infected branches often become swollen and with age may become deformed and highly branched. Aerial shoots appear within 2-7 years of infection and the female plant may produce single seeded fruit, which explosively discharges the seed (Smith 1971, Hawksworth and Wiens 1996, Mathiasen 1996). Although dwarf mistletoes are well studied, there is still much to know about their response to physical factors such as light, temperature, and humidity. These physical factors vary with height in forest stands and individual tree crowns (Parker 1995) and may affect several aspects of the life cycle of the mistletoe plant including; seed dispersal, seed germination, haustorium development, early growth of the endophyte, aerial shoot production, flowering, and pollination (Wagener 1961, Beckman 1964, Scharpf 1970, 1972, Wicker 1974, Knutson 1984, Hawksworth and Wiens 1996).

The influence of light on dwarf mistletoes has attracted limited study. Because partial thinning appears to favor rapid intensification of dwarf mistletoe, Weir (1916) suggested that dwarf mistletoes benefit from high light levels. Wagener (1961) has questioned this conclusion and demonstrated greater production under partial light than higher levels. Dwarf mistletoes may depend on light for seed germination (Wagener 1961, Beckman 1964, Scharpf 1970, Knutson 1984, Hawksworth and Wiens 1996), early growth of the plant (Wagener 1961, Scharpf 1972, Knutson 1984), and aerial shoot production (Knutson 1984) and light levels may be too low in some parts of the canopy for successful completion of the plant life cycle.

Knutson (1984) conducted 2 greenhouse experiments on several species of *Arceuthobium* to examine the influence of light and temperature on aerial shoot production. Mistletoe infected seedlings were exposed to various light and temperature regimes, and the development of the aerial

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shoots was observed under three levels of shading. The greatest number of aerial shoots was produced in low shade, but greatest cumulative length of aerial shoots was produced at low to medium shade. In a second experiment two light levels and three temperature regimes were used. The best development of aerial shoots was produced under high temperature and the lower light regime, leading Knutson to conclude that the effect of light seems indirect.

In a study at the Wind River Canopy Crane Research Facility, southern Cascade Mountains of Washington State, on adult sex ratio of hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones subsp. *tsugense*) Mathiasen and Shaw (1998) sampled 239 branches for mistletoe infections along the vertical axes of six western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) trees. Below 20 m in height, 53% of the infections did not have aerial shoots, while above 45 m, only 3% did not have aerial shoots. These data from Wind River suggested that there is a strong vertical gradient, along which production of aerial shoots from dwarf mistletoe infections increased with height. This supports observations by Smith (1969) that the quantity and vigor of shoots increased with increasing height in coastal western hemlock forests of British Columbia, Canada. Smith suggested that low light levels are responsible for reducing shoot production from infections in the lower canopy.

Plants higher in the canopy may not necessarily be receiving more light because light is heterogeneously distributed in time and space. To determine whether this is so, measurements or estimates of the forest light environment at each plant are necessary. This requires a means for reaching each plant and for quantifying the light environment in a meaningful way. Hemispherical photography provides a method for rigorously quantifying light environments in complex forest canopies (Anderson 1964, Rich 1990). From a single photograph of an evergreen forest, it is possible to measure overall canopy openness and openness along the sun track through the entire year. These measures of canopy structure can be directly transformed into relative amount of light, or absolute amounts if radiation data are available.

Hemispherical photography has been used to map fine scale horizontal variation in forest light environments (Becker and Smith 1989, Clark et al. 1996) but complete vertical access has proven problematic except in short forests (Lerdau at al. 1992). The Wind River Canopy Crane, a 75 m tall construction crane placed in an old-growth forest reserve to function as a canopy observatory, has been particularly useful in the study of dwarf mistletoes (Mathiasen and Shaw 1998, Shaw et al. 2000). The three-dimensional access provided by the Wind River Canopy Crane allows for sampling of numerous mistletoe infections even in the tops and outer canopy of 50 m tall trees. This canopy access technology is particularly suited for using hemispherical photography.

The objective of this study was to determine whether the observed vertical occurrence of aerial shoot production was related to the light environment associated with individual mistletoe infections. Hemispherical photographs allow several measures of the light environment in the forest canopy to be used to build predictive models of the presence/absence of aerial shoots. The results are then discussed with regard to the relative effectiveness of predictor variables, and some potential mechanisms and consequences of those relationships.

Study Site

The study site is located at the Wind River Canopy Crane Research Facility (Parker 1997) in the T.T. Munger Research Natural Area (Franklin and DeBell 1988), Wind River Experimental Forest, southern Cascade Mountains, Washington State (Latitude 45° 49' 13.76", Longitude 121° 57' 06.88") at an elevation of 355 m. A weather station was located 2 km south of the crane site at the now defunct Wind River Ranger Station, raw data was obtained from National Climate Data Center (1994) for the period 1931-1977. Annual precipitation was 2,467 mm, and is strongly seasonally distributed with summer precipitation averaging ~5% of the annual total. Average annual snowfall was 180 cm. Mean annual daily minimum temperature was 0.5°C, while mean annual maximum daily temperature was 12.3°C.

The forest is a tall stature Douglas-fir (*Pseudotsuga mensiezii* (Mirb.) Franco), western hemlock, and western redcedar (*Thuja plicata* Donn.) dominated stand with Douglas-fir reaching 65 m (average ht 52.2 m) and western hemlock reaching 55m (average ht 19.0 m). Stand density is 435 stems/ha with a basal area of 82 m^2/ha (Harmon

et al. 1998). The understory vegetation is dominated by vine maple (*Acer circinatum* Pursh), salal (*Gaultheria shallon* Pursh), and Oregon grape (*Berberis nervosa* Pursh), while the site is classified on the border of Western Hemlock/Oregon grape-Salal/Western Hemlock/Salal Plant Association complex and Pacific Silver Fir (*Abies amabilis* (Dougl) Forbes)/Salal Plant Associations (Meyer and Fredricks 1993). Soils are deep and well drained, derived from volcanic ejecta (Franklin 1972), and tentatively classified as medial, mesic Entic Vitrands (J. Klopatek, personal communication).

The light environment of this forest has been characterized by Parker (1997) and reflects the vertical structure of the forest, which is bottom heavy. He divided the canopy into three vertical zones: 1) a bright zone above 40 m in height where the light is 90% or more of available incoming light. 2) a transition zone from 40 m to about 8 m where available light drops steeply to about 10% of the incoming. 3) a dim zone below 8 m where light is less than 10% of the above canopy incoming. Western hemlock dominates the foliated portion of the canopy from 15 to 35 m, whereas western hemlock and Douglas-fir codominate the foliated canopy from 35 to 45 m, and Douglas-fir dominates above 45 m, with 80% of the stand foliage below 40 m (Parker 1997, Song 1998, Van Pelt and North 1999).

Methods

Infection Sampling

Infections were surveyed and sampled on 4 and 5 June 1998. Completely random sampling was not feasible given constraints on crane operations. A modified point-centered system was used. The gondola was placed over a gap between infected hemlock trees. At 5 m height intervals, the nearest infection on each tree was sampled. A total of 87 mistletoe infections on 14 trees were sampled, and heights ranged from 18 to 60 m. Sampling was restricted to mistletoe infections on live branches, implying the plant associated with the infection would also still be alive.

Mistletoe aerial shoot status was scored on a 0-3 scale. 0 meant no visible aerial shoots, 1 meant small poorly developed shoots <1 cm length, 2 meant many shoots, and 3 meant numerous robust shoots. For analysis purposes in logistic regression, 0-1 were considered "No Shoots", and 2-3 were considered "Shoots."

Hemispherical Photography

Hemispherical photographs were taken with standard procedures described in Rich (1989, 1990). Photos were taken through a Nikkor 8mm lens attached to a self-leveling platform (gimbals) on a monopod. Kodak TriX PAN 400 ASA black and white film was used. The gondola was maneuvered within reach of the chosen mistletoe infection and the camera assembly placed above the branch within 0.3 ms of the infection. A self-timer allowed the camera to steady at a level position, and the photograph was taken. Crane azimuth, hook height, and jib distance were recorded. Most photos were taken under dawn and overcast conditions, which allowed for acquisition of high quality images in which sky and foliage were well differentiated.

Photographs were analyzed with the program CANOPY 2.1 (Rich 1989), using standard procedures. Because the steel cage of the gondola precluded accurate compass measurements to orient the photos to true north, the azimuth of the crane jib was used for orientation. Following orientation of the negative to true north, the editing capabilities of CANOPY were used to remove the jib, cables, and other components of the crane and gondola. All photos were analyzed by one person (SBW).

Determination of the Light Environment

Standard "site factors" were calculated. Indirect Site Factor (ISF) is the proportion of sky visible from the photo point, and measures the penetration of diffuse radiation through the forest canopy. Direct Site Factor (DSF) is the proportion of the sunpath not obscured by foliage, weighted by a function of solar elevation angle to account for atmospheric transmissivity. Both ISF and DSF can be cosine corrected to a horizontal surface. In practice, cosine corrected and uncorrected site factors are highly correlated, and both were used in the initial analysis to find the best predictors of mistletoe shoot production.

Site factors can be converted into an estimate of total yearly (or monthly) radiation, if measures of direct and diffuse insolation are available (Rich et al. 1993). Shortwave insolation has been measured at Portland, Oregon, approximately 65 km

east southeast from the study site (National Renewable Energy Laboratory 1999). Insolation at the study site may differ slightly from that in Portland. The mean insolation for the year was calculated as a weighted sum of ISF and DSF:

$$1)\ \text{Insolation} = \text{Dif}*\text{ISF} + \text{Dir}*\text{DSF}$$

Yearly direct and diffuse shortwave insolation on a horizontal surface at Portland were 1779 and 1783 MJ $m^{-2}yr^{-1}$, respectively, and daily mean normal beam radiation was 4815 W $m^{-2}d^{-1}$. Global site factor for a horizontal collector (GSFC), therefore, is an equal weighting of ISFC and DSFC, while GSFU (uncorrected) is more heavily weighted by DSFU.

Statistical Analysis

Presence/absence of aerial shoots (dependent variable) was analyzed using logistic regression in JMP v. 3.0 (SAS Institute, 1995), with single predictor variables (Height, ISFC, ISFU, DSFC, DSFU, Mean yearly insolation) and goodness of fit (r^2) was used to compare the predictors. Logistic regression is a widely used technique for predicting presence-absence data from continuous independent variables (ter Braak and Looman 1995). Box plots were used for graphical comparisons.

Results

Four hemispherical photographs show key features of the forest light environment (Figure 1a-d). North is indicated by the N, and all sunpaths at this latitude are in the southern portion of the sky. The crane jib is clearly visible in the bottom three photos and provides azimuth orientation. Photo 1a is of a typically dark area below 30 m, where few plants produce shoots. Photo 1b was taken higher in the canopy on the north-side of a large tree, but DSF is relatively low because much of the yearly sunpath is blocked by foliage to the south. Photo 1c was taken on the south side of a large tree at 30 m, and shows a combination of low height and high insolation, because of high DSF. Photo 1d was taken at 46.7 m on the north side of a large tree with closely spaced tall neighboring trees.

A total of 89 infections were sampled: 41 had no aerial shoots (score 0 or 1), and 48 had substantial numbers of shoots (score 2 or 3). Mistletoe shoot production was significantly related to many predictor variables (Table 1). Height alone explained 42% of the variation in the logistic regression, with higher infections far more likely to have shoots than lower infections. All measures of the light environment from photographs explained more variance than height alone. The best single predictor was Insolation U (uncorrected), which explained 49% of the variation in shoot status. No significantly better results were obtained using multiple predictors such as monthly DSFs. Uncorrected site factors were slightly better than corrected, so all analyses and discussion will from now on consider uncorrected values.

The box plots show the overall distribution of height, ISF, DSF, and Insolation for plants with (score 2-3) and without (score 0-1) shoots (Figure 2). There is some overlap in all variables, but the good separation that visually confirms the results of the logistic regression (Table 1).

The relationships between height, insolation and mistletoe shoots are seen in detail in Figure 3. All infections above 50 m had shoots, and only one infection had shoots below 30 m. On the insolation scale, all infections with annual insolation above 3200 MJ m^{-2} yr^{-1} had shoots, and all infections with annual insolation below 1000 MJ m^{-2} yr^{-1} had none. From the logistic regression, the 50% probability of shoots is at 40 m, or at 2200 MJ m^{-2} yr^{-1}. Other probabilities are easily read off the logistic regression. In other forests, it may be easier to measure ISF and DSF, rather than using insolation data. Logistic regression parameters for ISF and DSF are presented in Table 1.

Discussion

Light is directly related to height in the canopy crane research forest, although the standard deviation of the mean PAR transmittance is highest between 15-30 m indicating the heterogeneity of the mid canopy environment (Parker 1997). Height and light are both good predictors of aerial shoot occurrence in this forest. However, total insolation, uncorrected for a horizontal surface, was the best predictor variable for the occurrence of aerial shoots, although the improvement in predictive power was moderate (from $r^2 = 0.42$ for height to 0.49 for Insolation). Both ISF and DSF alone also predicted shoot production slightly better than height alone.

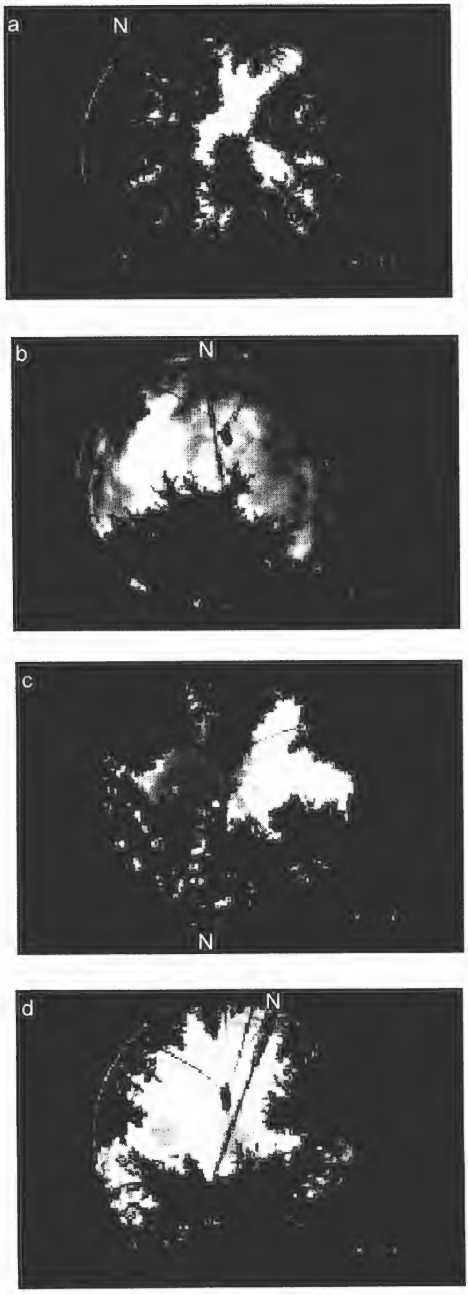

Figure 1. Four examples of photographs showing the range of conditions encountered in the study. North is indicated by the white "N". Note also that east and west are reversed on hemispherical photos taken directly upward. Height, ISF, DSF, Mean Daily Insolation, Crane Azimuth (AZ) and mistletoe score are shown next to each picture. See text for discussion of each photograph.

TABLE 1. Statistics of mistletoe predictor variables, the dependent variable is presence/absence of aerial shoots. Intercept (Int), regression coefficient (Coeff), and r^2 values are from nominal logistic regressions. All logistic regressions $P < 0.0001$.

Predictor	Int	Coeff	r^2	No Shoots		Shoots	
				Mean	s.d.	Mean	s.d.
Height			0.42	32	6.7	47	9.0
ISFU	4.11	-13.57	0.44	0.19	0.09	0.46	0.19
ISFC	4.80	-11.37	0.44	0.29	0.11	0.59	0.20
DSFU	3.12	-9.95	0.47	0.20	0.13	0.57	0.23
DSFC	3.54	-8.92	0.45	0.22	0.15	0.59	0.23
InsolationU	4.01	-0.00177	0.49	1290	745	3526	1418
InsolationC	4.74	-0.0033	0.49	890	420	2077	723

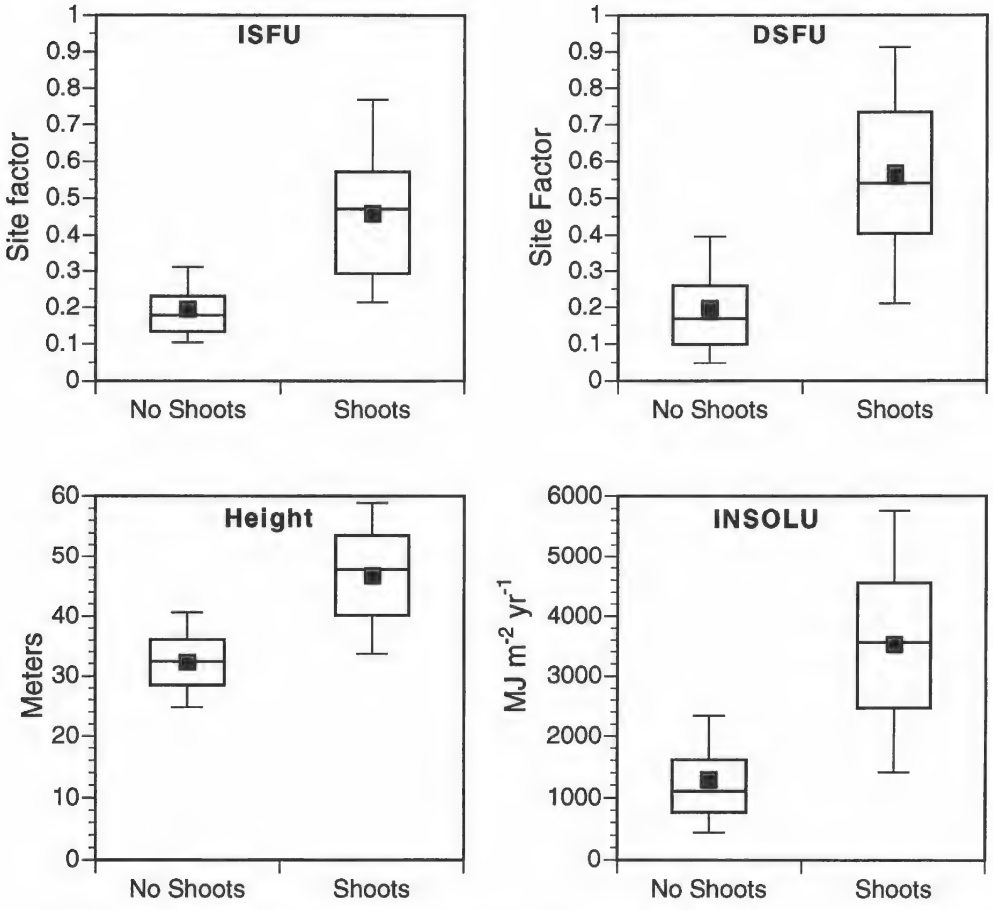

Figure 2. Box plots of predictor variables at 48 non-aerial shoot and 41 aerial shoot producing mistletoe infections. The square represents the mean, the middle line is the median, the outer lines of the box are the quartiles, and the outer bars are the 10th and 90th percentiles.

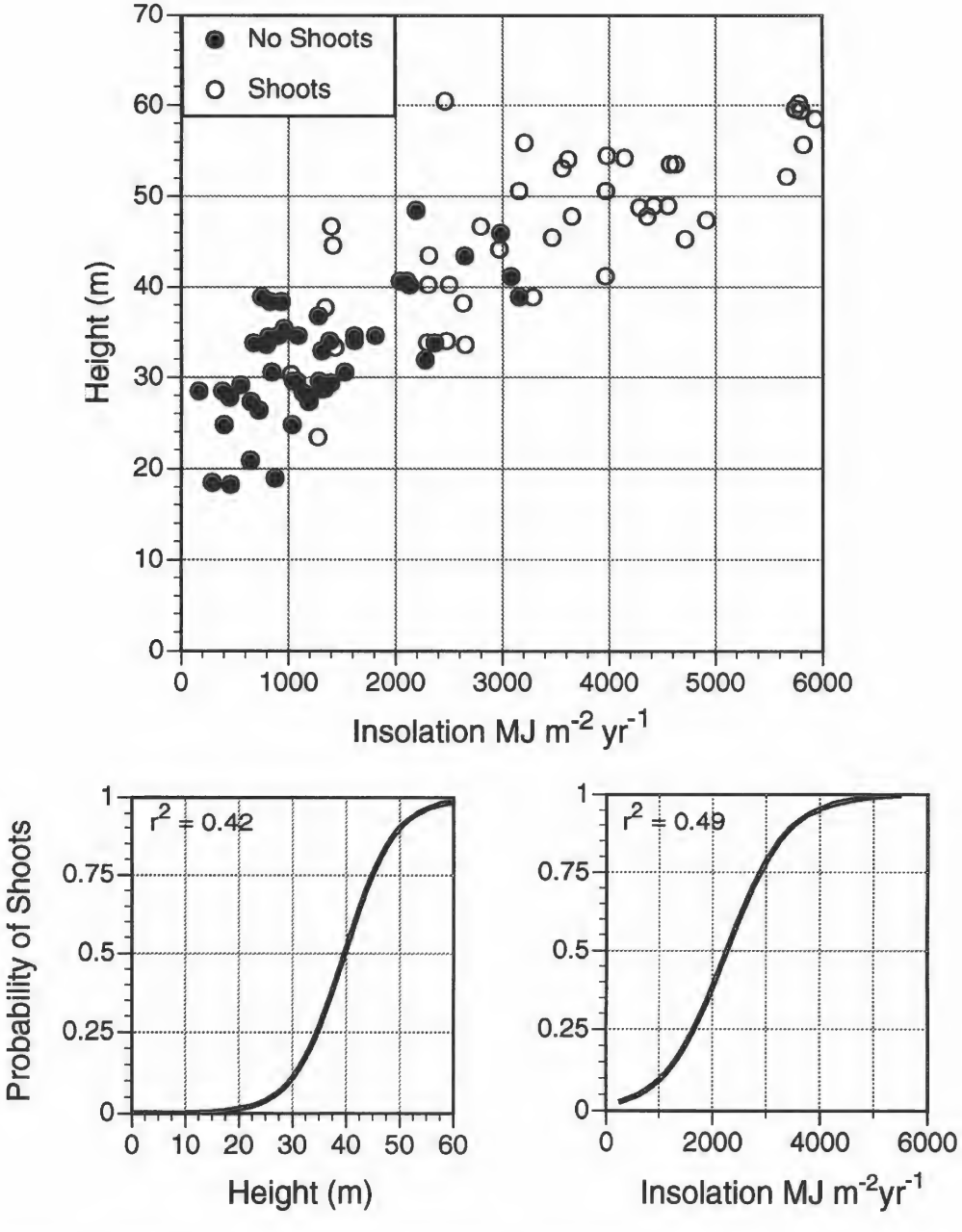

Figure 3. Insolation and Height plot showing the presence/absence of mistletoe shoots. Logistic regressions for Insolation and Height are shown below for parameters from Table 1.

Although ISF and DSF are highly correlated (r^2= 0.89), some sites (the north sides of large trees at intermediate heights (50-30 m) have high ISF and low DSF (e.g. Figure 1b). Conversely, DSF is higher on the south sides of trees (i.e. Figure 1c). There is likely a horizontal patterning of shoot production as one progresses from the north to south-sides of trees, and this pattern should be strongest at heights around 40 m in this forest where the overlap of shoots/no shoots is strongest (Figs 2c and 3).

There appears to be a paradox in reference to aerial shoot occurrence in the upper canopy. Our results support Weir's (1916), Gill's (1935), Smith's (1969) and Hawksworth and Wiens' (1996) observations that *Arceuthobium* "shoots seem to respond in vigor and abundance directly to the amount of light" (Gill 1935, page 216). However, experimental greenhouse studies on various *Arceuthobium* species, including *A. tsugense*, show that some light is necessary for aerial shoot development, but high light levels are not (Wagener 1961, Scharpf 1970, 1972, Tocher et al. 1984, Knutson 1984). Wagener (1961) states that, "if high light intensity is beneficial to dwarf mistletoe it must be exerted indirectly through its effect on the host tree." Why then, do aerial shoots occur mostly in the higher light levels of the transition and bright light zones of this forest?

A complex of biotic and abiotic factors associated with the vertical structure of forest canopies must be interacting to result in the observed patterns of mistletoe aerial shoot production that correlates with light and height. Knutson (1984) has determined, in greenhouse studies, that a high temperature and low light treatment resulted in greatest aerial shoot production. Because the highest temperatures are attained in the mid and upper canopy (Geiger 1965, Fitzjarrald and Moore 1995, Parker 1995), this region of the canopy may have the most optimal microenvironments for aerial shoot production.

Host plant physiology, especially the productivity of the foliage on the infected branches, may also play an important role in aerial shoot occurrence because of the nutrient and carbohydrate demands of mistletoe shoot growth. The foliage in the upper canopy has higher photosynthetic capacity and nitrogen content than foliage in the lower canopy (Holbrook and Lund 1995, Kozlowski and Pallardy 1997). Therefore, the occurrence of aerial shoots in the mid and upper canopy may be related to the capacity of the branch to "feed" the parasite. Finally, the evolutionary adaptations associated with flowering, pollination and seed dispersal in open and therefore sunny micro-environments may lead to the occurrence of aerial shoots in the upper canopy of this tall stature old-growth forest.

Implication for Spread and Intensification

Dwarf mistletoe reproduces by explosively discharged seed. Therefore, the composition and structure of the canopy in the immediate vicinity of the female plant has a controlling influence on the distance seed is dispersed, and whether the seed strikes host foliage or twigs (Scharpf and Parmeter 1976, Mathiasen 1996). Hemlock dwarf mistletoe aerial shoots occur mostly in the well-lit middle and upper canopy, above 30 m, with a 50% probability of aerial shoots occurring on a mistletoe infection at a height of 40 m, or at an annual insolation of 2,200 MJ $m^{-2}yr^{-1}$. The source of the seed rain from dwarf mistletoe plants is above the bulk of the hemlock foliage in a relatively open portion of the canopy, and this implies an ability to rapidly spread and intensify.

Dwarf mistletoe is known to spread and intensify most rapidly in multistoried canopies (Mathiasen 1996), and hemlock dwarf mistletoe is thought to spread rapidly in old-growth hemlock forests for this reason (Shea and Stewart 1972). The additional evidence that the seed source is primarily from the more open and well lit mid and upper canopy strengthens the conclusion that hemlock dwarf mistletoe is well adapted to complex structured old-growth canopy environments. Further research on the causes and consequences of the vertical organization of aerial shoot production in dwarf mistletoes will aid our understanding of mistletoe intensification and spread, especially in managed stands with long rotations or uneven-aged silviculture.

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The Effect of Multi-nutrient Fertilization on Understory Plant Diversity

Abstract

This study examined multi-nutrient fertilization effects on understory vegetation diversity at eight forested locations in the inland Northwest. Percent canopy covered by understory plant species of three growth forms (shrubs, forbs, grasses) and total understory were determined over a two year period following treatment. Two diversity indices (Shannon-Wiener index and Simpson's index) were used to quantify multi-nutrient fertilization effects on understory plant diversity. Multi-nutrient fertilization prescribed to increase overstory tree growth did not typically reduce understory vegetation diversity, rather diversity increased following fertilization on some sites. Understory composition at the time of treatment greatly determined fertilization effects on diversity as follows: 1) if most species in the plant community responded relatively the same after treatment, then diversity was unchanged even though total biomass increase may have been large; 2) if a highly responsive species was abundant prior to treatment, then diversity decreased following fertilization; and 3) if a highly responsive species was relatively rare prior to treatment, then diversity increased following fertilization. Multi-nutrient forest fertilization generally did not affect understory plant diversity, but where changes did occur, diversity increases were more common than decreases.

Introduction

Management of forest ecosystems to maintain and enhance biodiversity is becoming increasingly important in forestry (Burton et al. 1992, Lippke and Oliver 1993, DeWald and Mahalovich 1997) and one component of floristic diversity is understory species diversity. The understory plant community provides wildlife habitat (Holechek et al. 1995) and helps maintain a healthy ecosystem (Burton et al. 1992, Baskin 1994, DeWald and Mahalovich 1997). Fertilization is a forest management practice that is increasingly used to promote overstory tree growth and health (Shafii et al. 1989, Moore et al. 1991, Garrison et al. 2000). However, knowledge of fertilization effects on understory vegetation diversity is lacking.

Management practices that maintain a variety of successional stages, stand densities, overstory tree species, understory species, and stand structures in a mosaic of habitats across a landscape best maintain diversity (Hunter 1990). If fertilization directly increases diversity, or results in minimal decreases, then ecosystem diversity will be maintained while also obtaining increased growth rates of the tree overstory. However, understory species diversity decreases at higher overstory densities (Alaback and Herman 1988, Uresk and Severson 1989), and since fertilization increases overstory growth, one possible longer-term indirect effect may be a decrease in understory diversity.

Prescott et al. (1993) found that "nitrogen only" fertilization with rates greater than 100 kilograms per hectare decreased vascular plant species richness, while applications of "sulfur only", as well as sulfur combined with nitrogen, increased diversity. In the same study they also found that mixed fertilization decreased or did not change vascular plant richness in Douglas-fir (*Pseudotsuga menziesii*) stands in Washington. Abrams and Dickmann (1983) saw no significant changes in species richness following fertilization in jack pine (*Pinus lambertii*) stands in Michigan. Diversity may change as a result of certain plants being able to compete better than associates for the increased supply of nutrients following fertilization (opportunistic species), or some species could be eliminated due to nutrient toxicity (Chapin et al. 1986). Fertilization may indirectly alter competitive interactions if another factor, such as light becomes limiting. Our study does not directly address the physiological reasons for diversity change, but rather quantitatively documents if fertilization

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produced a change, thereby providing insight as to possible underlying factors associated with observed treatment differences. These observations should be of ecological interest and useful to land managers.

Methods

Eight different sites from five general locations, three in Idaho, and one each in Oregon and Washington were included in this study. The study sites are representative of mid elevation conifer forests in the inland Northwest with elevations ranging between 670 and 1245 m. A wide range of habitat types, tree densities, and overstory species were sampled (Table 1). Overstory tree species composition included natural, second-growth, mixed conifers as well as plantations composed of Douglas-fir and/or ponderosa pine (*Pinus ponderosa*). None of the study sites had any sort of cutting within the last 10 years.

Study Design

The study areas were designed to be fertilizer trials within much larger operational fertilization areas. Size of experimental areas ranged from 10 to 120 ha, and the physical arrangement of the various study sites differed resulting in variable numbers of transects per site (Table 1). The fertilizer and control treatments were randomly assigned to study stands within a site to the extent possible, given operational constraints. Fertilizers were applied aerially by helicopter and containers were placed throughout each treatment area to collect fertilizer. Collected fertilizer was then weighted to monitor and ensure even distribution throughout the study site. The fertilizer blends and treatment dates for each stand are provided in Table 1. We assume that the small differences in the micro-nutrient component of the fertilizer blends had no significant effect on understory response.

Aerial photographs were used to help determine the exact locations of the fertilized units and boundaries were marked for each treatment location. One hundred meter transects were established in both control and fertilized areas, with 13 m^2 sub-plots located every 10 m along a transect for a total of 11 sub-plots. Six to ten transects were placed in each stand to minimize variability within a transect as well as to capture variation across the treatment unit. A transect is the

TABLE 1. Selected site, stand, and treatment characteristics at the experimental locations.

Site	Dominant Overstory Species	Initial basal area[1] (m^2/ha)	Crown competition factor[1] (%)	Habitat series[2]	Treatment date	Multi-nutrient fertilizer blend (kg/ha)
Bovill, ID	Mixed conifer	30	286	red cedar	Fall 1997	N 220, K 110, S 88, Cu 11, B 5.5
Goldendale, WA	Douglas-fir & ponderosa pine	15	118	Douglas-fir	Spring 1997	N 220, K 220, S 88, Cu 11, Zn 11, B 5.5, Mo 1
New Meadows, ID	ponderosa pine	20	106	Douglas-fir	Fall 1996	N 220, K 220, S 88, B 11, Cu 11, Zn 11, Mo 1
Potlatch, ID	red cedar & grand fir	57	353	red cedar	Fall 1997	N 220, K 110, S 88, Cu 11, B 5.5
	Douglas-fir	5	16	red cedar	Fall 1997	N 220, K 110, S 88, Cu 11, B 5.5
	ponderosa pine	11	14	red cedar	Fall 1997	N 220, K 110, S 88, Cu 11, B 5.5
Wallowa, OR	Mixed conifer	16	103	grand fir	Fall 1995	N 220, K 220, P 110, S 99, B 11, Cu 11, Zn 11, Mo 1
	ponderosa pine	10	60	grand fir	Fall 1995	N 220, K 220, P 110, S 99, B 11, Cu 11, Zn 11, Mo 1

[1]Includes all tree species.
[2]After Steele et al. 1981 and Johnson and Clausnitzer et al. 1992.

sample unit in this study for both understory vegetation and overstory basal area measurements.

Vegetation Measurements

Three life forms were sampled: shrubs, forbs, and grasses, using the 13 m^2 sub-plots following protocols described in Moeur (1985). Sampling occurred in mid and late summer of 1997 and 1998. The exact sampling date differed by site to make plant phenological development stage similar between sites. We wanted to sample during the period of maximum understory production and again at the end of the growing season. Vegetation sampling plots were marked with a PVC pipe in the center. Variable radius overstory tree plots were centered on the vegetation plots to measure overstory tree density and species composition. Each measured tree was marked at diameter breast height (d.b.h.) measurement point to assist in future remeasurements. Average basal area per ha and crown competition factor (CCF) (Krajieck et al 1961) were calculated as the average of the transects for each treatment (Table 1).

Percent Cover and Vertical Layering Estimates

Understory percent canopy cover sampling procedures were taken from O'Brien and Van Hooser (1983). Crown canopy cover by height layers (0 to 0.5m; > 0.5 to 2.0m; and > 2.0m) was defined as the percent area of ground surface covered by the canopy of an understory plant. The canopy coverage for each recorded species was visually estimated and assigned to coverage classes (Daubenmire 1959) as follows: < 5, 5-25, 26-50, 51-75, 76-95, and > 95 percent. For each of the three plant groups (shrubs, forbs, and grasses), individual species information was collected for up to four species, each comprising a minimum crown canopy cover of 5 percent. Using this approach, a maximum of 12 individual species per plot was recorded. Confining the species list to the 12 predominantly occurring plant species on a plot makes field sampling efficient, yet still provides a good representation of the understory vegetation composition since many more than 12 species can occur on a transect and rarely were more than 12 species encountered on an individual plot during the study. Even so, the understory vegetation sampling methods (limited to 12 species per plot) may have truncated possible Shannon-Wiener index diversity values (Pielou 1966). Nomenclature follows Hitchcock and Cronquist (1976) for vascular plants studied. Grazed areas were excluded from the sites except for a light amount of cattle grazing at the New Meadows location.

Species Diversity Measures

We were interested in treatment effects on both abundant and rare plant species. Thus, species diversity was quantified using two diversity indices, the Simpson (Simpson 1949) and Shannon-Wiener (Peet 1974) diversity indices. Simpson's index, which is sensitive to changes in the most abundant species, is the probability of picking two plants randomly that are different species. Values range from 0 to almost 1 (Simpson 1949, Sullivan et al. 1998). Lower values indicate lower diversity. The Shannon-Wiener index is sensitive to rare species changes and quantifies the degree of difficulty in predicting the species of the next individual sampled. It increases with the number of species in the community, and ranges from 0 to approximately 5.0 (Peet 1974, Washington 1984). Higher values mean greater diversity. To better reflect understory biomass composition, species observations were weighted by their coverage percentage in calculating a weighted diversity index similar to the procedures of Sullivan et al. (1998).

Statistical Analysis

Understory plant diversity, as measured by either the Simpson (SI) and Shannon-Wiener (SWI) diversity indices, was the dependent variable in our analysis. Diversity indices were computed and analyzed separately for shrubs, forbs, and grasses, as well as collectively for all 3 growth forms. Transect estimates were averaged within each site and treatment, and these averaged data were then used in subsequent statistical analyses. The experiment was designed for using Analysis of Variance (ANOVA), and statistical comparisons between fertilizer treatments were conducted using PROC GLM of the Statistical Analysis System (SAS Institute Inc. 1985). The significance level chosen for statistical tests was 0.10, which is consistent with Sullivan et al. (1998). Goldendale, Bovill, and Potlatch 1997 data were not analyzed since the fertilization treatments at these locations occurred in late spring of that year.

Results

Diversity, as measured by the indices used, was determined by the weighted abundance of a particular species, as well as by the number of different species sampled in a treatment unit. Fertilization can affect both of these diversity determinants. Diversity changes due to fertilization were variable by plant growth form. Most SWI and SI results were consistent between both years and sampling periods within sites and growth forms, and led to the same conclusions regarding treatment effects on diversity. Thus, in the interest of brevity and clarity, we present results only for SWI. The 1998 analyses probably provide the most reliable results since all sites had one full growing season following treatment, thus our sample size is much larger in 1998 and extraneous variation due to fall versus spring fertilizer application is diminished.

Analysis of variance models and results are provided in Table 2. Fertilization produced different effects on overall plant diversity depending on the characteristics of the different study sites. Shrub, grass and combined growth form plant diversity for both years and forbs in 1998 differed by study site (Table 2). Treatment produced a significant main effect on combined growth form and forb diversity in 1998 but not in 1997. Grass

TABLE 2. Analysis of variance tables for Shannon-Wiener diversity index values by various understory plant growth forms for two study years.

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Combined growth forms 1997					
site	3	0.1830	0.0610	40.00	0.025
treatment	1	0.0075	0.0075	4.91	0.157
sample period	1	0.0011	0.0010	0.67	0.500
treat*period	1	0.0055	0.0055	3.62	0.197
site*treat	3	0.1232	0.0411	26.94	0.036
site*period	2	0.0752	0.0376	24.64	0.039
error	2	0.0031			
Shrubs 1997					
site	3	1.2570	0.4190	1233.84	0.001
treatment	1	0.1641	0.1641	483.32	0.002
period	1	0.0180	0.0180	52.98	0.018
treat*period	1	0.0081	0.0081	23.70	0.040
site*treat	3	0.1456	0.0485	142.94	0.007
site*period	2	0.0137	0.0069	20.17	0.047
error	2	0.0007			

continued, next column

TABLE 2, cont'd

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Forbs 1997					
site	3	0.0915	0.0305	1.04	0.525
treatment	1	0.0015	0.0015	0.05	0.844
period	1	0.1752	0.1752	5.95	0.135
treat*period	1	0.0097	0.0097	0.33	0.624
site*treat	3	0.0994	0.0332	1.13	0.502
site*period	2	0.2774	0.1387	4.71	0.175
error	2	0.0589			
Grasses 1997					
site	3	1.0964	0.3655	79.75	0.012
treatment	1	0.0930	0.0930	20.29	0.046
period	1	0.0060	0.0060	1.30	0.372
treat*period	1	0.0116	0.0116	2.53	0.253
site*treat	3	0.0745	0.0248	5.42	0.160
site*period	2	0.0135	0.0067	1.47	0.405
error	2	0.0092			
Combined growth forms 1998					
site	7	5.5134	0.7876	90.75	<.001
treatment	1	0.3080	0.3080	35.49	0.001
period	1	0.0059	0.0059	0.68	0.439
treat*period	1	0.0055	0.0055	0.63	0.452
site*treat	7	0.9459	0.1351	15.57	0.001
site*period	7	0.1994	0.0285	3.28	0.070
error	7	0.0608			
Shrubs 1998					
site	7	7.0938	1.0134	48.66	<.001
treatment	1	0.1036	0.1036	4.98	0.061
period	1	0.1239	0.1239	5.95	0.045
treat*period	1	0.0001	0.0001	0.01	0.943
site*treat	7	0.9588	0.1370	6.58	0.012
site*period	7	0.0478	0.0068	0.33	0.918
error	7	0.1458			
Forbs 1998					
site	7	2.6524	0.3789	49.98	<.001
treatment	1	0.2680	0.2680	35.34	0.001
period	1	0.1727	0.1727	22.78	0.002
treat*period	1	<.0001	<.0001	0.00	0.959
site*treat	7	0.8197	0.1171	15.44	0.001
site*period	7	0.3624	0.0518	6.83	0.011
error	7	0.0531			
Grasses 1998					
site	7	6.3636	0.9091	33.00	<.001
treatment	1	1.0273	1.0273	37.39	<.001
period	1	0.0020	0.0020	0.07	0.794
treat*period	1	0.0559	0.0559	2.03	0.197
site*treat	7	3.3941	0.4849	17.65	<.001
site*period	7	0.1798	0.0257	0.93	0.534
error	7	0.1923			

and shrub diversity was significantly affected by treatment in both years. Shrub diversity varied significantly by sampling period in both years. Forb diversity in 1998 also varied significantly by sampling period. A significant treatment by sampling period interaction was evident only for shrub diversity in 1997. Combined growth forms and shrubs showed a significant treatment by site interaction for both years and for forbs and grasses in 1998. The site by sampling period interaction term was significant for combined growth forms in both years, for shrubs in 1997, and for forbs in 1998.

Site specific least square mean estimates of SWI diversity by year, treatment, and sampling period for each understory plant growth form are provided in Table 3. Most statistical contrasts between treatments showed no significant change in diversity due to treatment. However, increases in SWI combined growth form diversity following fertilization were seen at the New Meadows site during late-summer for both years and mid-summer in 1997, as well as for the Douglas-fir plantation site at Potlatch for mid-summer. Shrub diversity increased after fertilization only at the western red cedar/grand fir site at Potlatch in mid-summer. For other site, year, sampling period combinations, shrub diversities remained the same or decreased. Forb diversity significantly increased for both sampling periods at the Douglas-fir plantation site at Potlatch. Significant increases in diversity occurred for grasses mid-summer 1998 at the New Meadows site, as well as the Potlatch Douglas-fir plantation site in both mid and late summer.

Decreases in overall growth form diversity, measured by SWI, were observed following fertilization in mid-summer 1998 at the Goldendale site (Table 3). Shrub diversity significantly decreased for both sampling periods in 1998 at the

TABLE 3. Shannon-Wiener (SWI) diversity indices mean values by treatment, plant lifeform, year, and sampling period for eight study locations in the inland Northwest.

			Combined		Shrubs		Forbs		Grasses	
Site	Year	Treatment	Mid	Late	Mid	Late	Mid	Late	Mid	Late
Bovill, ID										
	1998	Control	2.40	2.49	1.97	2.14	1.61	1.38	0.00	0.00
	1998	fertilized	2.90	2.69	1.74	1.98	2.14	1.99	0.00	0.00
Goldendale, WA										
	1998	Control	2.69	2.39	1.40	1.29	1.94	1.61	1.35	0.89
	1998	fertilized	2.45↓	2.23	0.80↓	0.85↓	1.83↓	1.24 ↓	1.30	1.38
New Meadows, ID										
	1997	Control	2.28	2.05	0.94	0.97	1.88	1.15	0.70	1.15
	1997	fertilized	2.53↑	2.28↑	0.81	0.76	2.02	1.48	1.17	1.48
	1998	Control	2.29	2.02	0.97	1.04	1.78	1.33	0.78	1.33
	1998	fertilized	2.56	2.35↑	0.70	0.85	1.85	1.25	1.38↑	1.25
Potlatch, ID										
red cedar/grand fir	1998	Control	0.88	0.79	0.18	0.29	0.68	0.66	0.00	0.00
	1998	fertilized	1.48	1.63	0.77↑	0.67	0.93	1.03	0.00	0.00
Potlatch, ID										
Douglas-fir	1998	Control	2.16	2.01	1.32	1.43	1.44	1.24	0.25	0.77
	1998	fertilized	2.68↑	2.81	1.48	1.64	2.10↑	2.12↑	1.35↑	1.64↑
Potlatch, ID										
ponderosa pine	1998	Control	2.39	2.29	0.95	1.16	1.70	1.62	1.03	0.91
	1998	fertilized	2.20	2.19	0.86	0.76↓	1.59	1.62	0.87	0.87
Wallowa, OR										
mixed conifer	1997	Control	2.18	2.34	1.43	1.60	1.47	1.61	0	0.15
	1997	fertilized	2.23	2.33	1.59	1.61	1.32	1.40	0.36	0.27
	1998	Control	2.30	2.41	1.65	1.63	1.43	1.56	0.17	0.33
	1998	fertilized	2.15	2.29	1.26	1.58	1.50	1.46	0.36	0.33
Wallowa, OR										
ponderosa pine	1997	Control	2.04	2.18	0.98	1.17	1.42	1.47	0.32	0.44
	1997	fertilized	1.94	1.91	0.62	0.72	1.68	1.24	0.43	0.58
	1998	Control	1.79	2.07	0.83	0.97	1.26	1.25	0.35	0.63
	1998	fertilized	1.84	2.05	0.42	0.68	1.34	1.42	0.36	0.77

↓↑ Arrows indicate a significant increase or decrease following treatment ($P < 0.10$)

Goldendale site, as well as late summer at the ponderosa pine plantation at Potlatch. Forb diversity significantly decreased at the Goldendale site. Grasses showed no significant diversity decreases due to fertilization at any location.

Discussion

Combined Growth Forms

Total understory diversity is a useful measure to quantify changes in the entire plant community following fertilization. Treatment effects were more pronounced in 1998 as nutritional differences had more time to manifest themselves in the plant communities. Site, treatment and their interaction were statistically significant for all growth forms in 1998. The significant site by treatment interaction derives from the result that only 3 of the 8 sites showed significant treatment effects. The New Meadows and Potlatch Douglas-fir sites increased in understory plant diversity, while at the Goldendale site, diversity decreased. Three factors contributed to the diversity increase at New Meadows: (1) grass diversity significantly increased after fertilization, (2) more species of all growth forms occurred in the fertilized area, and (3) the control showed little diversity, being substantially dominated by pinegrass (*Calamagrostis rubescens*) and elk sedge (*Carex geyeri*). Late-summer diversity also increased at this location in 1997 due to more grass and forb species being sampled in the fertilized area. The forb western yarrow (*Achillea millefolium*) was particularly abundant following fertilization, but remained at low levels in the control areas, which were dominated by pinegrass and elk sedge. Increases in combined growth form SWI diversity occurred for mid-summer in 1998 at the Potlatch Douglas-fir site due to an increase in common snowberry (*Symphoricarpos albus*) cover as well as by more grass species being sampled in the fertilized areas. Furthermore, the forbs speedwell (*Veronica* sp.) and clover (*Trifolium* sp.) were highly dominant in the control area causing relatively low diversity. Prescott et al. (1993) also found that common snowberry responded well to fertilization.

The understory component of the Goldendale site decreased in combined growth form diversity following fertilization because shrubs and forbs showed significant diversity decreases. The change in SWI was due to a large increase in percent cover for the shrub, squaw-carpet (*Ceanothus prostrates*) and the forb, hawkweed (*Hieracium* sp.), following fertilization. Nams et al. (1993) also showed increased growth for western yarrow after fertilization. Pinemat manzanita (*Arctostaphylos nevadensis*), common at this site, showed no response to fertilization, and this result is consistent with the lack of fertilizer response observed by Nams et al. (1993) for kinnikinnik (*Arctostaphylos uva-ursi*).

While changes in overall plant community diversity are important, individual growth form diversity changes are good indications of wildlife habitat differences (Holechek et. al. 1995). Changes in grasses and forbs will have more impact on grazing animals (i.e., cattle and elk) and changes in shrubs should have more effect on animals that are browsers (i.e. white-tailed deer) (Holechek et. al. 1995). Therefore, we analyzed shrub, forb, and grass diversity separately.

Shrubs

Minimal increases in shrub diversity were seen following fertilization. The only significant increase in shrub diversity occurred at the western redcedar (*Thuja plicata*)/grand fir (*Abies grandis*) site at Potlatch in the mid-summer sampling period but not in late summer (Table 3). Shrub diversity probably increased due to the presence of more species in the fertilized area, but this site exhibited low shrub diversity both before and after fertilization. Although statistically significant, actual changes in the understory under the dense tree canopy at this site were small.

Decreases in shrub diversity following fertilization occurred at two sites in our study. Shrub diversity decreased at the Goldendale site for both sampling periods in 1998 primarily due to a large increase in cover of squaw-carpet following fertilization. Late summer in 1998 also showed decreases in shrub diversity at the ponderosa pine plantation site at Potlatch because common snowberry increased in percent cover in the fertilized area.

Forbs

Forb diversity in mid and late summer increased only at the Potlatch Douglas-fir site. The diversity increase was due to speedwell and clover being less dominant in the fertilized area. Perhaps fertilization encouraged additional forb species to become established, but this is speculation.

Forb diversity decreased for the Goldendale site in mid and late summer 1998 following fertilization due to a large increase in hawkweed (*Hieracium* sp.) in the fertilized area. Forbs in the fertilized area were substantially dominated by hawkweed and western yarrow. Nams et al. (1993) also observed significant increases for western yarrow following fertilization.

Grasses

Grasses showed significant increases in diversity for mid-summer in 1998 at the New Meadows site and for the Potlatch Douglas-fir stand (Table 3). Diversity increases at both locations partially resulted from more grass species being sampled in the fertilized area. Possibly, establishment of new grass species was encouraged by fertilization; however, a more likely explanation is that *Poa pratensis* and *Stipa columbiana* exhibited a growth response to fertilization, thereby increasing their percent coverage and consequent inclusion in the sample.

Grasses showed no significant diversity decreases following fertilization at any study location. Therefore, fertilization to increase overstory tree growth should not significantly decrease grass diversity under mid elevation conifer stands in the inland Northwest.

All individual study sites were consistent in their diversity fertilization response across years and sampling periods. A site consistently increased, decreased, or remained unchanged. Most study sites showed no changes in overall diversity following fertilization. The Bovill site and both Wallowa sites showed no changes in overall diversity (Table 3) or for any growth form component of the understory. These sites had some of the same understory species that responded to fertilization at other sites that did show differences in understory vegetation diversity following fertilization. However, one striking difference between the Bovill site, as well as the Potlatch mixed conifer site, compared to all other locations was the complete absence of grasses in the understory. Perhaps combined life form diversity did not change following treatment at the Bovill site and the Potlatch mixed conifer site because of their high overstory conifer density, with CCF values of 286% and 353% respectively (Table 1). However, shrub diversity did increase under the very dense red cedar and grand fir canopy at the Potlatch location, but only for the mid-summer sampling. Although statistically significant for the mid-summer sampling, actual changes in shrubs at this site were small. Shrub diversity was very low prior to treatment and remained low following fertilization (Table 3). Other studies have found less diversity with increasing overstory density (Uresk and Severson 1989, Alaback and Herman 1989). We can only speculate about underlying causal factors that produced our results.

The significant treatment by site interaction means that fertilization effects on understory plant diversity differ by site, making generalizations difficult. However, we can make useful observations regarding pre-treatment differences in the plant communities that produced our results. Fertilization caused increases in understory diversity on two sites, a decrease on one site, and little or no change on the other five sites. Understory composition at the time of treatment greatly determines fertilization effects on diversity as follows: 1) if most species in the plant community respond relatively the same after treatment, then diversity may be unchanged even though total biomass increase may be large; 2) if a highly responsive species is abundant prior to treatment, then diversity may decrease following fertilization; and 3) if a highly responsive species is relatively rare prior to treatment, then diversity may increase following fertilization. Sites with high overstory density, such as the Bovill site, with a CCF of 286%, and the Potlatch mixed conifer location with a CCF of 353%, showed minimal change in combined life form understory diversity following fertilization. This is not surprising since these stands contained late-seral understory species which are adapted to tightly cycled nutrients (Tilman 1985), and they usually show lower response to an increased supply of nutrients (Grime 1977). The first type of response given above was observed at both Wallowa sites, and the second type of response occurred at Goldendale. Sites with moderate and low overstory basal areas showed both increase or decrease in diversity depending on the species present in the understory.

Of the three growth forms studied, grasses showed the least change in diversity following fertilization. Perhaps the grasses most common in our study, pinegrass and elk sedge, respond about the same to fertilization; therefore diversity

would not change after treatment. The results of Freyman and Van Ryswyk (1969) for pinegrass, and Riegel et al. (1991) for elk sedge, show that both species respond positively to fertilization. Forbs showed variable responses to fertilization, and western yarrow and hawkweed appear to be opportunistic forbs. Shrubs were also variable with respect to change in diversity following fertilization. Common snowberry seems to be an opportunistic shrub while pinemat manzanita appears not to be opportunistic. A species may respond on one site and not another for the following several reasons encountered in our study: 1) the presence of other, more competitive, understory species, 2) reduced fertilization response due to light or space limitation, or 3) general understory response may be affected by overstory competition. An example of the first two situations may be the grass response at the Goldendale site being limited by low growing shrubs. An example of the third case would be low understory biomass available to show appreciable response at the Potlatch high overstory density western red cedar/grand fir site.

An important issue for resource managers in the inland Northwest is the presence of noxious weeds. Fertilization has the potential to increase not only desirable but also undesirable understory species. In our study hawkweed generally increased in both biomass and relative abundance following fertilization. The species of hawkweed we encountered were *Hieracium albiflorum* and *H. albertinum* rather than the exotic, noxious members of this genus.

Conclusions

Many factors may affect understory response to fertilization and consequent change in understory community diversity. Results from our study suggest that little change in understory diversity will occur in stands with higher overstory density. Therefore, applying multi-nutrient fertilization in mid elevation forests of the inland Northwest to increase overstory growth of these stands normally targeted for operational forest fertilization may not greatly affect understory vegetation diversity. Furthermore, understory composition at the time of treatment greatly determines fertilization effects on diversity as follows: 1) if most species in the plant community respond relatively the same after treatment, then diversity may be unchanged even though total biomass increase may be large; 2) if a highly responsive species is abundant prior to treatment, then diversity may decrease following fertilization; and 3) if a highly responsive species is relatively rare prior to treatment, then diversity may increase following fertilization. In our study the following individual species can be characterized as responsive to multi-nutrient fertilization: the shrubs, *Symphoricarpos albus* and *Ceanothus prostratus;* the forbs, *Achillea millefolium, Fragaria* sp., and *Hieracium* sp.; and the grasses, *Deschampsia* sp., *Festuca occidentalis,* and *Poa pratensis.* We do not intend to imply that the above plant list is exhaustive for those that are responsive to fertilization, merely that these plants showed response in our study. Multi-nutrient fertilization has many positive benefits for a forest community and in our study, in most cases did not drastically reduce understory vegetation diversity. On some sites, understory vegetation diversity increased following fertilization.

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Distribution of Grizzly Bears in the U.S. Northern Rockies

Abstract

The current estimated distribution area of grizzly bears (*Ursus arctos*) in the U.S. Northern Rockies suggests they have recently expanded their distribution in this region. Expansion beyond designated recovery zones has important conservation and land management implications. Using a computer home range program, HOME RANGER, and about 3,000 recorded locations of grizzly bear observations obtained from numerous state and federal agencies, current distribution of grizzly bears was estimated as an aid to recovery efforts. I estimated the distribution area of grizzly bears in the U.S. Northern Rockies at about 102,524 km^2. This is significantly larger than previously reported by other sources, and greatly exceeds the 56,043 km^2 area delimited as grizzly bear recovery zones by the U.S. Fish and Wildlife Service. I suggest there is merit in expanding designated recovery zones. Greater research and management attention must be paid to peripheral areas as range expansion by bears may outpace management response, with potentially negative consequences to both bears and humans.

Introduction

The grizzly bear (*Ursus arctos*) was listed as a threatened species in the contiguous U.S. states pursuant to the federal Endangered Species Act in 1975. Grizzly bears now occur on less than 2% of their historic distribution area (U.S. Fish and Wildlife Service 1993) in the contiguous states. The U.S. Fish and Wildlife Service (1993, 2000) has identified five grizzly bear recovery zones within the U.S. northern Rockies: the Northern Continental Divide, Yellowstone, Cabinet-Yaak, Selkirk, and Selway-Bitterroot areas (Figure 1).

The central goal in recovery planning for threatened and endangered species is to increase both the numbers and distribution of the species. Current information on the distribution of grizzly bears is therefore vital to the design and implementation of management programs to ensure survival of the species, recovery of viable populations, and reductions in bear/human conflicts. The bounds of animal populations should initially be delimited based on animal locations (Craighead, et al. 1995). Merriam (1922) and Mattson, et al. (1995) have provided estimates of distribution area for the contiguous states and other investigators have described distribution for discrete population areas (Basile 1982; Dood, et al. 1986; Blanchard, et al. 1992). Here I describe a larger area of distribution for grizzly bears in the U.S. northern Rockies than has previously been given and I suggest the current extent of recovery zones be re-examined.

I address three fundamental questions: 1)What is the current distribution of grizzly bears in the U.S. northern Rockies?; 2) How does this distribution compare with recovery zones designated by the U.S. Fish and Wildlife Service?; 3) Is there merit to enlarging the recovery zones?

Methods

The area analyzed is the U.S. northern Rockies generally bounded by the 49° and 42° N. latitudes and 119° and 108° W. longitudes, shown in Figure 1. A Geographic Information System (GIS), Arc/Info 7.11 and ArcView 3.0 with Spatial Analyst (Environmental Systems Research Institute 1997) were used to plot digitized locations and for spatial analysis. Two categories of data were used to estimate current grizzly bear distribution. These were: 1) digitized data used with a home range program to construct distributional isopleths; 2) undigitized observational data used for comparison with the isopleths.

Construction of Isopleths

I used the program HOME RANGER Version 1.0 (Hovey 1998) and the adaptive kernel method, to construct 95%, 96%, 97%, 98%, 99%, and 100% isopleths for the Yellowstone, Northern Continental Divide, Cabinet-Yaak, and Selkirk areas, to represent distribution areas. HOME RANGER has a larger capacity (two billion data points) than other home range estimators such as CALHOME (Kie, et al. 1996), making HOME RANGER more

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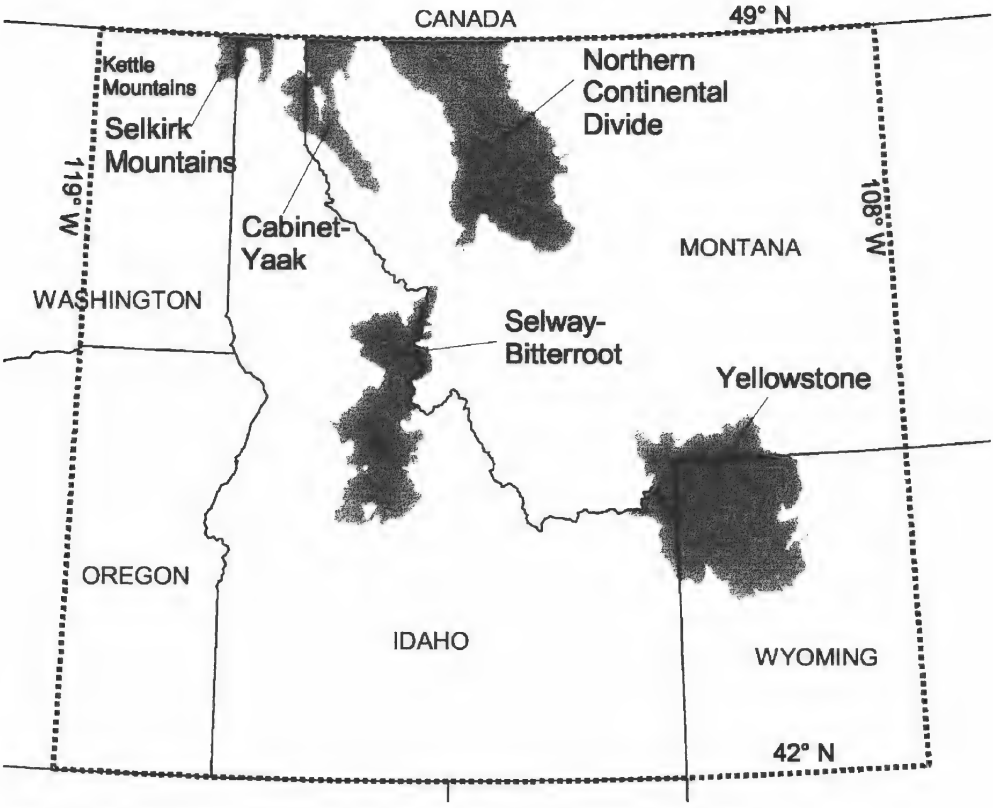

Figure 1. The Northern Rockies Study Area and the Locations of Grizzly Bear Recovery Zones.

useful for this work since two of the data sets had n > 500.

I used data from grizzly bear observations recorded by state and federal wildlife management agencies and expressed as Universal Transverse Mercator (UTM) coordinates, that were digitized and plotted. In cases where there was more than one source of data for an area, the data were pooled. For the Yellowstone area (n = 1,426), sources for recorded locations were Craighead, et al. (1988); Dood and Pac (1993); Pac and Dood (1999); Gunther, et al. (1992-1997). For the Northern Continental Divide area (n = 418), sources were Dood and Pac (1993); Pac and Dood (1999). Sources for the Cabinet-Yaak area were Groves (1987) and digital data provided by the U.S. Fish and Wildlife Service (n = 871). Sources for the Selkirk Mountains were the Washington Department of Wildlife (1998), and digital data provided by the Idaho Department of Fish and Game (n = 138). The source for the Salmon-Selway-Bitterroot region of north-central Idaho was Groves (1987), and for the Kettle Range in northeast Washington was the Washington Department of Wildlife (1998). However, data from central Idaho were relatively sparse (n = 81) and collected in the period from 1930 to 1985 and in the Kettle Range of northeastern Washington, total observations (n = 5) were low. Thus, not enough data points from recent observations were available for construction of HOME RANGER-based isopleths and no results are reported for those two areas.

The UTM coordinates used were approximate and may contain error. For example, most Cabinet-Yaak data had a 100 m resolution (within 100m of the "true" location), but some data points had up to 1 km resolution (W. Kasworm, U.S. Fish

and Wildlife Service, pers. comm.). I considered this level of error acceptable at the population area level, which encompassed thousands of km^2.

Different types of observations were used to increase sample sizes. By each area these were: Yellowstone, locations of mortalities, management actions, and conflicts; Northern Continental Divide, locations of mortalities and sightings of females with cubs; Cabinet-Yaak, observations from sighting reports and mortalities; Selkirk Mountains, observations from sighting reports. Outlying data points were evaluated for their temporal distribution to ensure that estimated distribution was current, as opposed to historic. Areas with observations from both the 1980s and 1990s were considered part of the current distribution area. Comparison data from observations prior to the 1980s (historic) were used to detect potential increases in distribution area. Portions of the Northern Continental Divide, Cabinet-Yaak and Selkirk isopleths within Canada were excluded from size calculations since the purpose of this work was to estimate distribution in the U.S. northern Rockies. As an additional approximation of distribution, areas adjacent to the isopleths were examined and based on my best judgment were adjusted where they were identified as occupied grizzly bear habitat by state fish and game agencies or other sources.

Data Used for Comparison with the Isopleths

To check the accuracy of my results from HOME RANGER, I used a wide array of mostly undigitized data sources for comparison (Table 1). Non-digital comparison data could not be used for construction of isopleths because the locations were approximate and UTM coordinates were not available. Thus, I duplicated these non-digital data on transparent overlays and placed those on top of maps including HOME RANGER isopleths for comparative analysis.

Results

The 99% isopleths constructed using HOME RANGER best described distribution (Figures 2, 3, 4, and 5). Based on the comparative analysis, the 95-98% isopleths underrepresented distribution and excluded numerous locations of females with cubs (resident bears) and the 100% isopleth overrepresented distribution by including vast land areas of unoccupied habitat between outlying points. Thus, the 99% isopleth represents an estimated distribution boundary for grizzly bears, with verified observations of bears occurring at some unknown frequency beyond these bounds.

By summing the area encompassed by the 99% isopleths and adding portions of three additional areas (Yellowstone, Selkirk Mountains and Cabinet-Yaak areas) to this total, I estimated a distribution area for grizzly bears in the U.S. northern Rockies at about 102,524 km^2 (Figure 6; Table 2). In the Yellowstone area a portion of the Teton and Gros Ventre Ranges just south of the isopleth, and the Tobacco Root Mountains to the northwest of the isopleth were added based on a map of 1998 distribution provided by the Wyoming Game and Fish Department (D. Moody, pers. comm.). In the Selkirk Mountains an area to the south and west of the main isopleth was added to incorporate observations from the late 1990s including a documented female with cubs. Small adjustments were made to the periphery of the Cabinet-Yaak isopleth to incorporate recent observations. This broader boundary provides no information on the density, population trend or health of the populations within, and it encompasses areas that may be occupied sporadically, at low frequency and at low densities. For the smaller Cabinet-Yaak and Selkirk geographic areas, the 99% isopleth was adjusted for sample size, which adjusts the *ad hoc* smoothing factor, *h*. This reduced the buffer distance around the periphery of the locations, and I concluded this better represented distribution.

My estimated distribution area exceeds by about 46,476 km^2 the area encompassed by the recovery zones with the largest additional area in the Yellowstone region and the least in the Selkirk Mountains. Only in the Northern Continental Divide region did my estimated distribution substantially coincide with the recovery zone, with the exception of the east side (Figure 6). Agricultural activity and human settlement bracket this recovery zone on the west and east. Grizzly bears expanded their distribution area in the Yellowstone region during the 1980s and 1990s to the south and southeast of the recovery zone. Expansion occurred to the east of the Northern Continental Divide recovery zone and may now be occurring in the Selkirk Mountains.

TABLE 1. Data used for Comparison with the HOME RANGER Isopleths.

Area	Data Type	N	Years Collected	Source
Yellowstone	Recorded Observations Outside Yellowstone National Park	144	1970-1974	Knight, et al. (1975)
Yellowstone	Reported Sightings	349	1975-1977	Knight, et al. (1976-1978)
Yellowstone	Verified Observations	1,073	1973-1979	Basile (1982)
Yellowstone	Verified Observations	701	1980-1984	Knight, et al. (1981-1985)
Yellowstone	Map of All Verified Observations	N/A	1980-1989	Blanchard, et al. (1992)
Yellowstone	Recorded Initial Locations of Females With Cubs	248	1988-1997	Knight, et al. (1989-1993); Knight & Blanchard (1994-1996); Knight, et al. (1997); Haroldson, et al. (1998)
Yellowstone	Recorded Observations	33	1983-1989	McDonald, et al. (1990), shown in Craighead, et al. (1995)
Yellowstone	Composite Home Ranges of Radio-collared bears	57	1975-1987	Knight, et al. (1988)
Yellowstone	Composite Home Ranges of Radio-collared bears	26	1975-1998	Provided to author by Wyoming Game & Fish Department
Yellowstone	Estimated Distribution	N/A	1998	Provided to author by Wyoming Game & Fish Department
Targhee National Forest	Summary of Observations	181	1965-1984	Orme & Williams (1986)
Northern Continental Divide	Recorded Locations of Mortalities	288	1970-1984	Dood, et al. (1986)
Northern Continental Divide	Total Recorded Observations from the Rocky Mountain Front	3,587	1976-1985	Aune, et al. (1986)
Northern Continental Divide	Composite Home Ranges of Male & Female Radio-collared bears	28	1977-1987	Aune & Kasworm (1989)
Northern Continental Divide	Composite Home Ranges of Radio-collared bears on the Blackfeet Reservation & Glacier National Park	7	N/A	Carney (1990), shown in Dood & Pac (1993)
Northern Continental Divide	Composite Home Ranges of Male & Female Radio-collared bears	50	1987-1995	Mace & Waller (1998)
Cabinet-Yaak	Composite Home Ranges of Male & Female Radio-collared bears	18	1983-1994	Kasworm & Servheen (1995)
Selkirk	Composite Home Ranges of Male & Female Radio-collared bears	11	1983-1993	Provided to author by Idaho Fish & Game Department

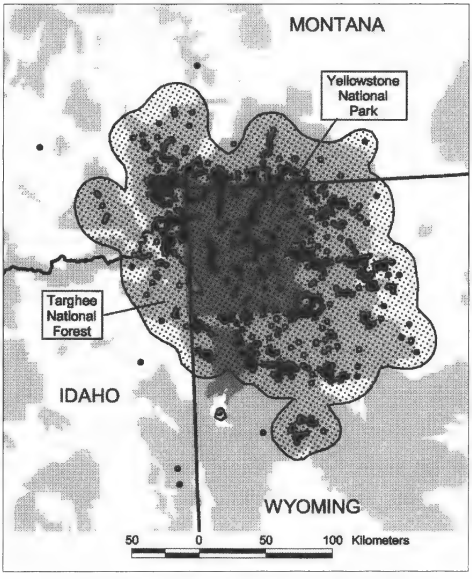

Figure 2. HOME RANGER 99% Isopleth, Yellowstone Ecosystem.

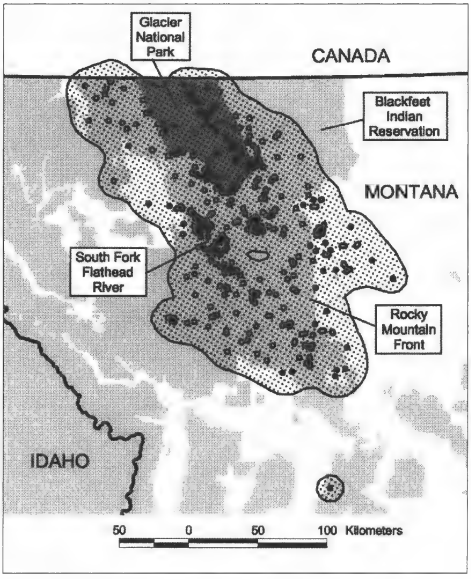

Figure 3. HOME RANGER 99% Isopleth, Northern Continental Divide Ecosystem.

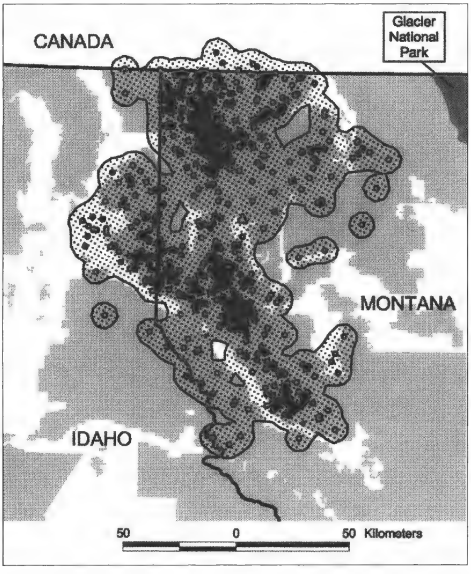

Figure 4. HOME RANGER 99% Isopleth, Cabinet-Yaak Ecosystem.

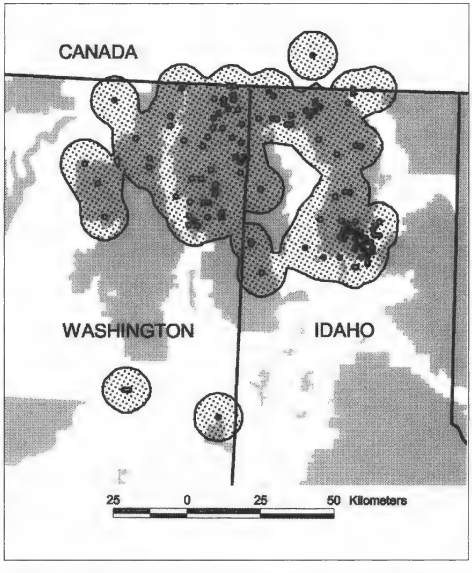

Figure 5. HOME RANGER 99% Isopleth, Selkirk Mountains Ecosystem.

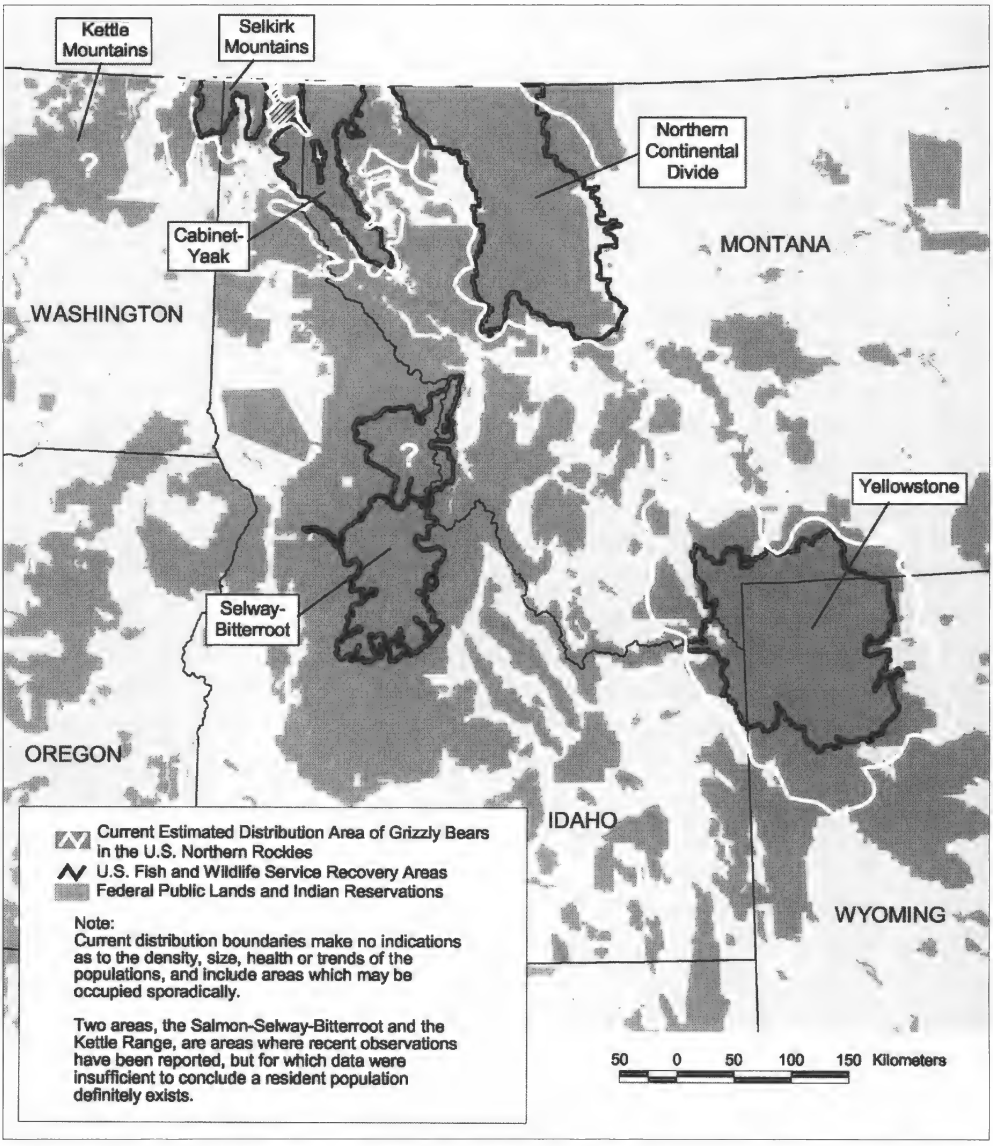
Kettle Mountains
Selkirk Mountains
Northern Continental Divide
Cabinet-Yaak
MONTANA
WASHINGTON
Yellowstone
Selway-Bitterroot
OREGON
IDAHO
WYOMING
Current Estimated Distribution Area of Grizzly Bears in the U.S. Northern Rockies
U.S. Fish and Wildlife Service Recovery Areas
Federal Public Lands and Indian Reservations
Note:
Current distribution boundaries make no indications as to the density, size, health or trends of the populations, and include areas which may be occupied sporadically.
Two areas, the Salmon-Selway-Bitterroot and the Kettle Range, are areas where recent observations have been reported, but for which data were insufficient to conclude a resident population definitely exists.
50 0 50 100 150 Kilometers

Figure 6. Current Estimated Distribution of Grizzly Bears in the U.S. Northern Rockies.

Two areas, the Salmon-Selway-Bitterroot in north-central Idaho and the Kettle Range in northeast Washington, may support very small populations or the occasional dispersing individual although recent observations provide evidence of grizzly bears in the Kettle Range (Washington Department of Wildlife 1998) and a potential source population occurs across the Canadian border (Horejsi 1999) and sightings of grizzly bears continue to be reported in the Salmon-Selway-Bitterroot (Lolo National Forest 1998). My results also show significant overlap among the Northern

TABLE 2. Area (km^2) for the 95-99% Isopleths. Areas calculated using ArcView 3.0 to display HOME RANGER isopleths. Internal islands not included in totals. All external islands included in totals except for two from Canada from the Cabinet-Yaak ecosystem. *Adhoc h* = 5.0.

	Isopleth				
Area	99%	98%	97%	96%	95%
Yellowstone	43598.3	36217.5	32477.0	29831.3	27818.6
NCDE	33666.6	30061.7	27685.6	25796.8	24364.6
Cabinet-Yaak[1]	14694.3	12762.4	11559.8	10467.4	9684.1
Selkirk Mountains[1]	6387.4	5524.3	5064.6	4654.4	4332.4
Total	98346.5[2]	84565.9	76787.0	70749.8	66199.8

[1]*Adhoc h* adjusted for sample size by HOME RANGER.

[2]Three areas were added to the 99% isopleths which resulted in a total estimated distribution area of 102,524 km^2.

Continental Divide, Cabinet-Yaak, and Selkirk distribution areas and I suggest they may be biologically linked, although due to the low density of locations within the overlap zone, the connection may be tenuous. Merriam (1922) considered this as a single population.

The locations of radio-collared grizzly bears and mortality locations provided the most reliable information, as location and species were confirmed. Larger sample sizes, longer duration of data collection, and larger amounts of comparison data gave me greater confidence in these results. Thus, I have highest confidence in the Yellowstone distribution results, and least in the Selkirk Mountains. I am confident I did not overestimate distribution because observations of females with cubs, management actions and mortalities have occurred beyond the isopleths.

Discussion

Should Recovery Zones Be Enlarged?

Grizzly bear recovery zone boundaries, with a few modifications, date to when grizzly bear populations were at a historic low point which precipitated protection under the Endangered Species Act. Thus, potential expansions in distribution area have significant implications for conservation management of the species. Based on recent history in Wyoming, there can be a lag time between expansion and detection or acknowledgment by managers, which leaves large gaps in management efficiency and success. Moreover, significant expansions beyond the recovery zones results in a bifurcated management regime where some portions of grizzly bear populations receive full legal protection under the Endangered Species Act, whereas other portions receive reduced protection or no protection. Bears occurring outside recovery zones receive no formal consideration by the U.S. Fish and Wildlife Service pursuant to Section 7 of the Endangered Species Act on projects which may adversely modify habitat and/or elevate mortality risks. Other differences include no food storage orders for backcountry users such as hunters and hikers and no restrictions on road density and vegetation cover standards specific to grizzly bears. Failure to document or account for grizzly bear presence may increase the chances of surprise encounters between humans and bears. Higher risks/rates of conflict may reduce human tolerance for grizzly bears thereby increasing bear mortality and overall risk to the species.

Lower or nonexistent standards for grizzly bear habitat protection may result in the impediment of movements among isolated populations, thus preventing a key conservation goal. The smaller recovery zones limit potential increases in total population size, a critical factor in conservation of the species for both demographic and genetic concerns. Allendorf and Ryman (In press) report that the effective population size (N_e) to total population size (N) ratio for grizzly bears is about 1:5 and long-term persistence may require approximately 5,000 individuals in a single population or meta-population. Applying the 1:5 N_e:N to the total population recovery goal (U.S. Fish and Wildlife Service 1993, 2000) for the five northern Rockies recovery zones (N = 1,026 with the Bitterroot, where reintroductions are being considered, and N = 746 without it), the recovery zones in sum would support $N_e < 250$, far less than the minimum $N_e = 500$ cited by numerous

investigators (Frankham, 1995; Nunney and Campbell, 1993) for minimum species viability. I argue these are compelling reasons for expanding the designated recovery zones, necessary to meet basic conservation goals for the species.

Capture and Data Bias Issues

With access to locations of radio-collared bears obtained via telemetry, my estimates of distribution, particularly in the Yellowstone area, would have likely resulted in a smaller estimated distribution area. For example, Blanchard and Knight (1991) reported 6,299 radio-relocations of 97 radio-collared bears between 1975-1987 in the Yellowstone area, with most inside Yellowstone National Park. Due to the large number of locations in the center of the area, the result would be an imploded distribution boundary for isopleths < 100% using HOME RANGER. This phenomenon reveals the effects of study area and capture bias in wildlife research studies. For practical and budgetary reasons, most grizzly bear core study areas are located within higher productivity habitats to increase trapping success and sample sizes (Metzgar and Bader 1992; Mattson 1997) and many study areas are much smaller than the recovery zone (Wielgus, et al. 1994; Mace and Waller 1997; U.S. Fish and Wildlife Service 1999). Overflights are generally limited to the recovery zones with minimal effort to document bear distribution beyond the periphery (C. Schwartz, Interagency Grizzly Bear Study Team, pers. comm.). Study effort has also moved from year to year (Blanchard, et al. 1992). Thus, the distribution area of a population based exclusively on data obtained from radio-collared animals may be significantly underestimated, unless capture bias issues are resolved within the overall study design. Otherwise, there is less ability to detect expansions and contractions in distribution area since peripheral areas are not routinely sampled. I argue for a concerted effort to document bear distribution and status in areas beyond the current recovery area boundaries to gain a more comprehensive view of the populations.

Conclusions

I provided evidence that the distribution of grizzly bears in the U.S. northern Rockies is significantly greater than is circumscribed by recovery zones outlined in the Grizzly Bear Recovery Plan (U.S. Fish and Wildlife Service 1993). Whereas a significant amount of this area encompasses private lands, large portions of their distribution was located on federal public lands. Although it is unrealistic to expect grizzly bear recovery throughout their historic range, I argue that the size and boundaries of recovery areas should be expanded and critical habitat designation should be considered, particularly on public lands. Lands currently outside the recovery areas receive no special consideration as grizzly bear habitat within the land management planning process. Enlarging the recovery zones will also provide additional opportunities for management on private lands where inclusion could foster cooperation and coordination between public and private landowners thus increasing the potential for recovery and sound management. Increasing the amount of habitat area is necessary to meet all seasonal requirements in order to expand the grizzly bear population to viable levels.

The estimated distribution areas for the Northern Continental Divide, Cabinet-Yaak, and Selkirk areas show overlap, suggesting that interchange between these populations is possible, although in no way should this suggest that the Cabinet-Yaak and Selkirk populations are not at critically low population size ($n < 50$). The data do indicate that measures should be taken to enhance the connection between these areas, including enlarging and managing the three areas as one recovery area.

Programs that estimate the home range of a species have utility in estimating distribution areas for populations, depending on the nature of the available data, the existence of comparison data sets, and familiarity with the home range characteristics and life histories of the species under study. There is a level of error associated with any method used to estimate population distribution or individual home ranges, particularly for wide-ranging, low density species such as grizzly bears. However, I believe the method I used provided reasonably accurate results. Combined with locations from radio-collared grizzly bears and annual updating, this method could provide a quick and relatively simple system for tracking of distribution trends for grizzly bears, reducing lag effects and the need for periodic, dramatic management interventions.

An annual assessment of distribution is particularly important given there is significant annual variation in individual grizzly bear ranges depending on weather and major food source availability (Mattson 1997). During drought years and major food source failures, bears make use of areas which may not be used during good food source years. Recovery planning could be improved by incorporating these sporadically used, but occasionally critical habitats.

More systematic, uniform, and unbiased methods of obtaining and recording grizzly bear observations are needed to more accurately and frequently estimate distribution of the species. Failure to pay more attention to expansions and contractions of grizzly bear distribution could leave significant portions of remaining grizzly bear populations subject to unnecessary risks and could delay detection of range collapse so that management interventions are untimely.

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The Northern Flying Squirrel (*Glaucomys sabrinus*) as a Potential Predator of Marbled Murrelet (*Brachyramphus marmoratus*) Eggs.

Abstract

Marbled murrelet (*Brachyramphus marmoratus*) populations have been declining in North America for over a decade. As a result, the bird was listed as threatened by the U.S. Fish and Wildlife Service in 1992. Nest predation has been posed as one reason for the decline and several forest rodents, including northern flying squirrels (*Glaucomys sabrinus*), are potential nest predators. We investigated whether the northern flying squirrel was capable of preying upon eggs similar in size to marbled murrelet eggs. We determined whether sex or age at capture from the wild affected a squirrel's tendency to attack an egg. We exposed a captive colony of northern flying squirrels to multiple experiments using a single egg from bobwhite quail (*Colinus virginianus*), blue grouse (*Dendragapus obscurus*), pigeon (*Columba livia*), and chicken (*Gallus domesticus*) with chicken eggs being most similar in size to marbled murrelet eggs. Age at capture and sex of squirrels did not influence predatory behavior. We found that flying squirrels were only able to break through eggs quail-sized and smaller, so flying squirrels are unlikely predators of marbled murrelet eggs. Both gape of the mouth and eggshell thickness could limit egg predation, so eggs with thinner shells and eggs smaller than quail eggs are potential prey for flying squirrels.

Introduction

During the later part of the 20th century, marbled murrelet (*Brachyramphus marmoratus*) populations have been declining in North America (Ralph et al. 1995), and in September, 1992 the U.S. Fish and Wildlife Service listed the species as threatened in Washington, California, and Oregon. Certain researchers believe that marbled murrelets are declining in Alaska (Piatt and Naslund 1995, Piatt 1998), but others believe that definitive evidence for the decline is lacking (Hayward and Iverson 1998a,b). Potential causes for the decline in the United States include pollution and oil spills, habitat loss due to the reduction and fragmentation of late successional forests, and predation at the nest (Ralph et al. 1995).

Marbled murrelets most often nest in the forest canopy at a height ranging from 57.4 ± 8.2 to 73.1 ± 10.4 m in Washington, Oregon, and California (Nelson 1997) making murrelet nests vulnerable to avian and arboreal mammalian predators. Marbled murrelets leave the nest unattended while foraging, which may also increase probability of predation (Nelson and Hamer 1995). Marbled murrelets in the Pacific Northwest nest upon natural platforms with a mean length of 320 mm and a mean width of 220 mm covered in pre-existing litter, moss, and lichen which serves as nesting material (Hamer and Nelson 1995). Birds then place their eggs in a depression in the nesting substrate. Predators of marbled murrelet eggs include the common raven (*Corvus corax*), the Steller's jay (*Cyanocitta stelleri*), certain accipiters, several species of forest owls, rodents, and potentially, the American crow (*Corvus brachyrhynchos;* Nelson and Hamer 1995). Northern flying squirrels are most abundant in forests typical of murrelet nesting habitat (Carey 1996), and are reputed to eat eggs and nestlings (Wells-Gosling and Heaney 1984). In addition, northern flying squirrels have been photographed in the wild preying upon quail eggs (Vander Haegen and DeGraaf 1996). Marzluff et al. (1999) frequently photographed them at artificial marbled murrelet nests, suggesting that northern flying squirrels may commonly encounter bird nests.

Given that egg size may limit the ability of rodents to prey upon eggs (i.e. DeGraaf and Maier 1996; Roper 1992, but see Craig 1998), we tested

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the ability of a captive colony of northern flying squirrels to open eggs of different sizes to determine if marbled murrelet eggs are vulnerable to nest predation by the squirrels. We then determined a threshold egg size beyond which squirrels could not open eggs. We also determined if predatory behavior varied by sex or the age at which squirrels were taken into captivity.

Materials and Methods

We simulated marbled murrelet nests by constructing nest platforms that were 229 mm wide by 310 mm long with slight edges on each side to keep eggs from rolling off the platforms. We placed a mat of *Bryoria* spp. lichen on the simulated nest platform and placed a single egg in a depression in the lichen because marbled murrelets lay a single egg (Nelson and Hamer 1995). On multiple occasions, we exposed a captive colony of flying squirrels to the simulated nest containing an egg from chicken (*Gallus domesticus*), blue grouse (*Dendragapus obscurus*), pigeon (*Columba livia*), or northern bobwhite quail (*Colinus virginianus*). The width and length of each egg was measured before each trial and eggshell thickness values were obtained after each trial using dial calipers (SPI, model 31-415). Grouse and pigeon eggs were collected from wild nests in western Washington, chicken eggs were purchased from a supermarket, and quail eggs were obtained from a private breeder in Wyoming.

We used a captive population of 15 northern flying squirrels held at the University of Wyoming in Laramie, WY, during experiments. Squirrels were held indoors in an enclosure approximately 2.7 m tall, 3.7 m wide, and 2.4 m long, but were exposed to ambient temperature and light via an open window. The enclosure contained five nest boxes and two trees held by metal tree stands. Most squirrels were collected from the Payette National Forest in central Idaho in the summers of 1996-1998. Five males and five females were captured as adults. One male and three females were captured as juveniles, whereas one male was born in captivity in July 1998. All squirrels were full grown adults at the time of the trials. Pregnant and lactating females were removed from all trials to avoid infanticide.

Prior to observation, each squirrel in the colony was marked with non-toxic permanent markers on the ventral side to distinguish sex and age at capture. The squirrels were fed *ad libitum* Purina rodent feed along with nuts, mushrooms, and *Bryoria* spp. lichen. For each trial, an observer entered the enclosure approximately 20 minutes before sunset and attached the nest platform to a tree and placed a single egg on the platform. The platform and egg were easily viewed from outside the enclosure using red lights and an ultraviolet light. Animals were observed during their first evening activity period only. Egg type, time of emergence from boxes, foods available to the animals, age class of individuals present, absent individuals, time and duration of each visit to the nest platform, the sex and age at capture of each animal that visited the platform, and the behavior observed at the platform were recorded. Animals classified as adults were greater than a year old at capture and juveniles were less than a year old at capture. Observation lasted the duration of the first activity period, usually two to three hours and ceased when most animals returned to the nest boxes. Trials were conducted from March through August 1999.

Statistical Analyses

We compared egg width and eggshell thickness among bobwhite quail, pigeon, blue grouse, and chicken eggs and used a one way ANOVA with Tukey-Kramer multiple comparisons on the means (Zar 1974). We used chi square test of homogeneity (Jelinski 1991) to determine if the tendency to bite an egg was independent of age at capture and sex of squirrels. We grouped squirrels based on sex and age at capture and compared groups based on the number of biting visits to the total number of animal nights (number of nights observed multiplied by the number of squirrels in each category observed per night) for age at capture and sex based on the outcome of the tests for effects of sex and age. We used chi square analysis to determine (1) the effect of egg type on success in breaking the egg and (2) the effect of egg type on the attraction of squirrels to eggs. Egg attractiveness was determined by the ratio of platform visits that involved biting to overall platform visits by egg type. In addition, we calculated the total time (in seconds) that squirrels were attempting to bite each egg type and the total time that squirrels were on the platform for each egg type. Given the time spent on the nest platform, we examined the proportion of time biting the

egg and time not biting the egg and then tested the proportion on egg types using a Z approximation of a binomial distribution (Zar 1974). For all analyses, we used a = 0.05 to determine significance.

Results

Eggs differed in width ($F = 259.71$, df = 3,15, $P < 0.001$) and eggshell thickness ($F = 31.58$, df = 3,19, $P < 0.001$). In general, eggshell thickness increased with egg size. Quail eggs had a width of 19.42 ± 0.77 (SE) mm, pigeon eggs were 29.54 ± 0.59 mm wide, grouse were 37.75 ± 0.94 mm wide, and chicken eggs were 42.31 ± 0.44 mm wide. Eggshell thickness values were: quail, 0.11 ± 0.02 mm, pigeon, 0.27 ± 0.02 mm, grouse, 0.33 ± 0.03 mm, and chicken, 0.37 ± 0.01 mm. All possible multiple comparisons were significantly different for egg width, but eggshell thickness results yielded four significant comparisons; Quail-Pigeon, Quail-Grouse, Quail-Chicken and Pigeon-Chicken. Quail eggs were significantly different from all other egg types for both egg width and eggshell thickness (Table 1).

Tendency to bite an egg was not affected by squirrel age at capture ($\chi^2 = 0.40$, df = 1, $P = 0.94$) or sex ($\chi^2 = 1.96$, df = 1, $P = 0.58$). As a result, we pooled results from all squirrels for remaining analyses. Squirrels were attracted to eggs equally, regardless of egg type ($\chi^2 = 4.34$, df = 3, $P = 0.23$), but quail eggs were successfully eaten more often than the other egg types ($\chi^2 = 26.67$, df = 3, $P < 0.001$); squirrels were successful in breaking through only quail eggs. When comparing the proportions of time biting egg and time on platform by egg type, interesting patterns emerge (Table 1). Quail eggs were not handled for long periods of time because squirrels were successful in breaking through these eggs quickly. Of unopened eggs, squirrels spent significantly more time attempting to open the smallest eggs, suggesting that they considered smaller eggs to be a food source more than larger eggs.

TABLE 1. Comparison statistics for egg types. For pairwise comparisons of proportions of time biting egg compared to total time on platform by egg type, t statistics and P-values are given. For multiple comparisons on egg width and eggshell thickness, values are differences in means.

Comparison	t statistic (P value)	Egg Width	Eggshell Thickness
Quail-Pigeon	13.33 (0.006*)	-10.12*	-0.15*
Quail-Grouse	6.38 (0.024*)	-18.33*	-0.22*
Quail-Chicken	2.73 (0.112)	-22.89*	-0.26*
Pigeon-Grouse	20.87 (0.002*)	-8.21*	-0.06
Pigeon-Chicken	21.29 (0.002*)	-12.77*	-0.10*
Grouse-Chicken	8.18 (0.015*)	-4.56*	-0.04

* denotes significance at $\alpha \leq 0.05$.

Discussion

Northern flying squirrels were able to penetrate bobwhite quail eggs, but were not able to break through larger and thicker-shelled eggs. Rodents may be gape-limited in their ability to open eggs (i.e., DeGraaf and Maier 1996; Roper 1992). If gape limits the ability of northern flying squirrels to open eggs, marbled murrelet eggs are likely safe from predation by squirrels, for our squirrels could not open eggs that were considerably smaller (pigeon eggs) than those of marbled murrelets which are 37.6 ± 1.4 mm (SD) in width and 59.8 ± 2.2 mm (SD) in length (Nelson 1997). Hypothetical gape limitations, however, should be considered with caution, for recent work suggests that rodents may open eggs of a size larger than their gape should allow. Blight et al. (1999) found that *Peromyscus* sp. on Triangle Island off British Columbia opened eggs of rhinoceros auklets (*Cirorhinca monocerata*), despite these eggs being much larger than their gape should allow. Craig (1998) showed that chipmunks (*Tamias* spp.) use leverage to open quail eggs by orienting eggs between their bodies and the nest until the small end is exposed. Chipmunks then break through the small end of the egg. We did not observe flying squirrels using leverage to break open eggs. Squirrels would hold eggs in their forepaws and occasionally hold eggs next to their bodies, but the eggs did not touch the edge of the nest platform while squirrels were trying to break through. These conflicting results suggest that a complete understanding of egg predation by rodents will require further experimentation.

In this study, quail eggs (shell thickness of 0.11 ± 0.02 mm) were potential prey for flying squirrels, but pigeon eggs (shell thickness of 0.27 ± 0.02 mm) were not. These results suggest that the threshold eggshell thickness for predation by flying squirrels lies between 0.11 ± 0.02 mm and 0.27 ± 0.02 mm. Given that this threshold range includes the marbled murrelet shell thickness of

0.21 mm (Sealy 1975), marbled murrelet eggs may be potential prey for flying squirrels, especially if eggshell thickness determines success of egg predation. However, it is likely that eggshell thickness and egg width interact to determine whether a mammalian predator can open an egg. Therefore the large size of marbled murrelet eggs in combination with their eggshell thickness likely prevent flying squirrels from opening these eggs.

The tendency and ability of our squirrels to consume smaller eggs suggests that northern flying squirrels may be significant egg predators of many forest-nesting passerines, particularly those with eggs smaller than pigeon eggs. This is supported by work with captive squirrels in Washington state, where Bradley and Marzluff (unpublished data) showed that northern flying squirrels will readily consume eggs from zebra finches (*Taeniopygia guttata*; eggs 15.8 ± 0.03 (SE) mm x 10.8 ± 0.03 mm, shell thickness = 0.076 ± 0.001 mm), yet cannot open small chicken eggs (eggs 50.3 ± 0.25 x 39.1 ± 0.18 mm, shell thickness = 0.256 ± 0.002). It is unlikely that adult passerines could successfully defend their nest against a flying squirrel (Bradley and Marzluff, unpublished data).

In conclusion, it is unlikely that northern flying squirrels are capable of preying on marbled murrelet eggs. If squirrels are gape-limited in their ability to prey on eggs, those of marbled murrelets are too large to be opened, for our egg width threshold was less than that of a marbled murrelet egg. However, if the ability of squirrels to prey on eggs is limited by the thickness of the shell alone, marbled murrelet eggs may be vulnerable to predation by northern flying squirrels; our shell thickness threshold range included the thickness reported for marbled murrelet eggs. We believe that both eggshell thickness and egg size determine predation success and as a result flying squirrels are likely unable to break open marbled murrelet eggs. Our results show that northern flying squirrels are capable of preying on eggs quail-sized and smaller, suggesting that they may be nest predators of small, forest-nesting passerines.

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Detecting Wildlife Orthologues for Tumor Necrosis Factor (TNF) and Interleukin-6 (IL-6)

Abstract

Detection and quantification of cytokines is important to better understand disease processes in populations. This study assessed the feasibility of quantifying wildlife orthologues for tumor necrosis factor (TNF) and interleukin-6 (IL-6) using two bioassays combined with an *in vitro* model for immune stimulation. For all species, heparinized blood (1 ml) was exposed to lipopolysaccharide (LPS; 10 pg to 50 μg) for 6 hr (37°C) after which plasma was collected. Neutralizing antibodies were used to demonstrate that grizzly bear (*Ursus arctos*) TNF can be quantified with a WEHI-164 bioassay, and expression of TNF in the LPS stimulated model is dose-dependent. A B9 bioassay demonstrated LPS-dose-dependent production of IL-6 for grizzly bears, although neutralizing antibodies were not available to confirm that IL-6 was responsible for these results. The B9 assay may have detected IL-6 orthologues for bighorn sheep (*Ovis canadensis canadensis*), elk (*Cervus elaphus*) and bison (*Bison bison*). These assays combined with the LPS stimulated blood model could provide a rapid means for assessing immunological effects of pathogens and toxicants.

Introduction

Cytokines are low molecular weight proteins that play a significant role in human and mouse immunopathology (Remick and Friedland 1997). The ability to quantify orthologous cytokines in wildlife will be an important step to developing a better mechanistic understanding of disease processes in these species. In this paper we assess the feasibility of quantifying two pro-inflammatory cytokines in several wildlife species. Tumor necrosis factor (TNF) plays a significant role in initiating an inflammatory response in human and mouse models of disease. Interleukin-6 (IL-6) is also associated with inflammatory events and has been used as an indicator of severity of septicemia in humans (Damas et al. 1992). In this paper we studied the production of cytokines in whole blood; this could serve as a nondestructive *in vitro* system for assessing effects of antigens and toxicants on immune systems of wildlife species.

Quantifying cytokine concentrations usually involves either an enzyme-linked immunoassay (ELISA) or a bioassay (Remick and Friedland 1997). ELISAs provide information about the presence of proteins of interest, but provide no information about the biological activity of these proteins. In addition, ELISAs typically employ antigen specific antibodies that are rarely suitable for interspecific assays. Alternatively, bioassays provide information about the biological activity of the protein of interest and they tend to be more suitable for interspecific assays. For instance, the WEHI cytotoxicity assay described below has been used to quantify TNF in humans (Call and Remick 1998), mice (Ebong et al. 1999), and several species of domestic livestock (Su et al. 1992, Ellis et al. 1993, Egan et al. 1994, Boury et al. 1997). In this paper we used two bioassays in conjunction with a whole blood model (Strieter et al. 1990) to quantify TNF and IL-6 in several wildlife species.

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Methods

Up to 25 ml of blood was collected into heparinized tubes from captive grizzly bears (*Ursus arctos*; n = 4), bighorn sheep (*Ovis canadensis canadensis*; n = 1), elk (*Cervus elaphus*; n = 1) and bison (*Bison bison*; n = 1). The choice of these species was based on their ready availability at the time of this study. All animals appeared to be in good health. Blood was also collected from normal human volunteers (n = 4) into heparinized syringes. Grizzly bears were housed by the Washington State University Bear Program, Pullman, Washington. Remaining wildlife were maintained at the Idaho Fish and Game Wildlife Health Laboratory, Caldwell, Idaho. All animal husbandry practices and protocols for blood collection were approved by the host Institutional Animal Care and Use Committees. Protocols for collection of human blood were approved by the Institutional Review Board, University of Michigan, Ann Arbor, Michigan.

Within 1 hr of collection, 1 ml heparinized blood was aliquoted into 1.5 ml microcentrifuge tubes and stimulated with between 10 pg and 50 µg lipopolysacharride (LPS, Sigma, St. Louis, Missouri). LPS is a component of Gram negative cell membranes and it typically induces leukocytes to rapidly upregulate expression of pro-inflammatory cytokines. The LPS (50 mg/ml) was stored frozen in RPMI-1640 media (RPMI; BioWhittaker, Walkersville, Maryland) and the same lot was used for all experiments. RPMI alone was used as a negative control. Blood was then held for 6 hr at 37°C with gentle agitation every 30 min. After incubation, samples were centrifuged (2000 × *g*, 5 min) and plasma was collected for analysis.

TNF bioactivity was assessed using the WEHI 164 subclone-13 bioassay (Espevick and Nissen-Meyer 1986). The WEHI cells (mouse macrophages) undergo lysis when membrane-bound TNF receptors are activated. Consequently cell death can be used as an indicator of the presence of biologically active TNF. Two replicates of each plasma sample were serially diluted (1:10 initial dilution and 1:2 subsequent dilutions) across 96-well cell culture plates (Costar, Cambridge, MA) in 100 µl of dilution media (RPMI, 1% fetal calf serum (FCS), 1 mM L-glutamine (BioWhittaker)). Trypsinized WEHI cells (5×10^5 cells/ml) were resuspended in suspension media (RPMI, 10% FCS, 1 mM L-glutamine, 3 µg/ml gentamicin (Sigma)). Actinomycin D (0.5 µg/ml; Calbiochem, La Jolla, California) was also included in the suspension media to halt cell proliferation during subsequent incubations. The cell suspension was added to the sample dilutions (1:1) and held overnight (37°C, 5% CO_2, humidified chamber). At approximately 18 h, cell viability was assessed by adding tetrazolium salt WST-1 (WST; 1:63 final dilution; Roche Diagnostics Corporation, Indianapolis, Indiana) followed by an additional 6 h incubation. Absorbance was quantified at 465 nm (630 nm background subtraction) using a BioKinetics plate reader (Bio-Tek Instruments, Winooski, Vermont) where higher absorbance correlated with greater cell viability and reduced levels of TNF. A standard curve was fitted to absorbance from serial dilutions (1:2) of recombinant human TNF (Cetus Corp, Emeryville, California) and used to quantify sample TNF. This assay was suitable for quantifying TNF between 1-2 pg/ml to 150 pg/ml.

Neutralizing antibodies were used to determine if cytolytic activity of bear plasma was due to TNF. The assay was conducted as described above except wells were prepared with anti-mouse-TNF (amTNF; 0.5% final concentration) serum, or control serum. Individual wells included either a 1:40 dilution of plasma from bear blood treated with 10 ng LPS, or a 1:40 dilution of plasma from bear blood treated with RPMI, or 375 pg recombinant human TNF.

IL-6 bioactivity was assessed using the B9 cell bioassay (Aarden et al. 1987). When IL-6 receptors are activated, these cells undergo rapid proliferation. Two replicates of each plasma sample were serially diluted (1:10, 1:2) across 96-well cell culture plates in 100 µl dilution media (Iscove's modified Dulbecco medium (BioWhittaker), 5% FCS, 1 mM L-glutamine, 100 U/ml each of penicillin and streptomycin (Gibco BRL)). Stock cultures were resuspended (5×10^5 cells/ml) in the above media plus 100 µM 2-mercaptoethanol (Sigma). The cell suspension was added to the sample dilutions (1:1) and incubated three days at 37°C (5% CO_2, humidified incubator). WST was added (1:63 final dilution) and after 6 h absorbance was quantified as described above. We used serial dilutions (1:2) of human recombinant IL-6 (PeproTech, Rocky Hill, NJ) to construct a standard curve with a minimum sensitivity of 1-2 pg/ml).

Results and Discussion

Both human and grizzly bear leukocytes had similar patterns of TNF production in response to increasing doses of LPS (Figure 1). The absolute activity of grizzly bear TNF appeared to be 50-fold lower than human TNF levels when blood was treated with 10 ng LPS. We expected that inherent differences in orthologous proteins would elicit different levels of cytolytic response from the WEHI cell line. Alternatively, the antigenic activity of the LPS used in this study may be weak for bear leukocytes. Consequently, while relative comparisons are meaningful, estimates of absolute TNF concentrations in different wildlife species would require species specific standard curves in the assay.

It is possible that residual LPS or some other protein in grizzly plasma produced a similar cytolytic effect unrelated to TNF concentration. To test this latter hypothesis, bear plasma was incubated in the bioassay with a polyclonal antibody (rabbit) that neutralizes the biological activity of both human and mouse TNF (Remick et al. 1990). Normal rabbit antisera was used for control treatments. As expected, human TNF treated with control antibody was not neutralized (low absorbance) while neutralizing antibodies blocked the cytolytic activity of the human TNF (Figure 2; high absorbance). A similar pattern was observed for LPS treated bear plasma and these results were replicated using a second neutralizing antibody (rabbit anti-human TNF; data not shown). Plasma from bear blood treated with RPMI showed no effect from either antibody treatment. These results demonstrate that the WEHI bioassay was responsive to TNF rather than experiencing cell death due to exposure to residual LPS or other unidentified proteins. These results also suggest that our antibodies would also be useful for immunohistochemistry with bear tissue. We were unable to detect any TNF in bighorn sheep, elk or bison plasma with the WEHI assay (data not shown).

Both human and bear leukocytes produced similar levels of IL-6 in response to increasing doses of LPS (Figure 3). These results might be explained by mitogenic effects of residual LPS contained in the plasma, except the B9 bioassay does not experience increased cell proliferation in the presence of LPS (Ulich et al. 1994). We did not have access to neutralizing antibodies against IL-6, but the dose-dependent response was consistent with

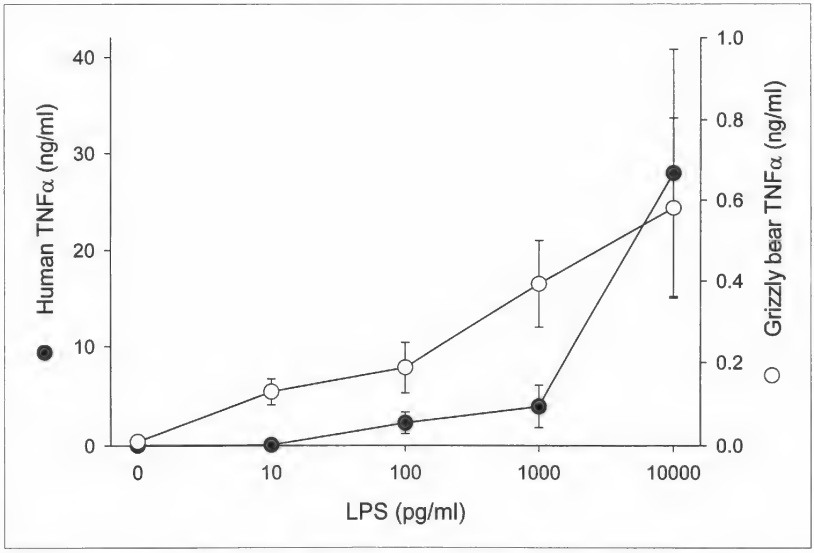

Figure 1. Absolute quantity of human (black circle, left axis) TNF and relative quantity of grizzly bear TNF (open circle, right axis) based on the WEHI bioassay. Data (avg ± SEM) were collected from an LPS-stimulated whole blood model involving four replicate donors for both human and bear experiments. Quantity of TNF was based on serial dilutions of human recombinant TNF and may not reflect absolute concentrations of bear TNF.

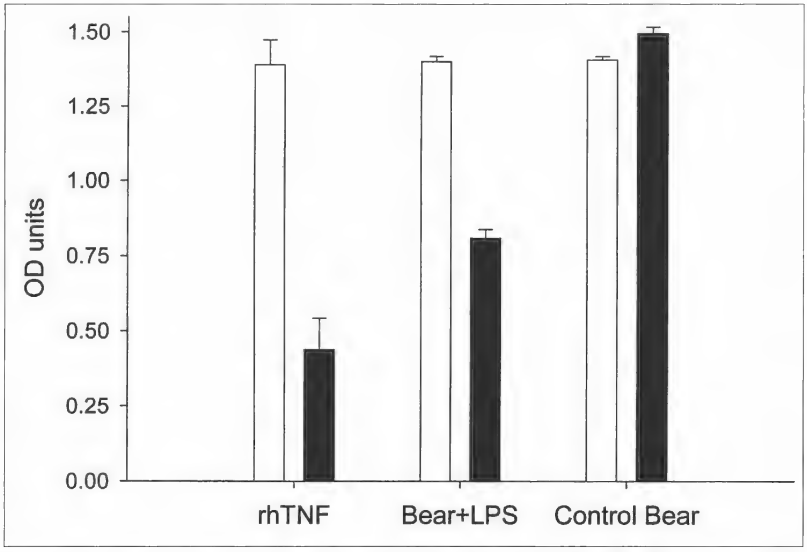

Figure 2. Effect of neutralizing antibodies on cytolytic activity of human and bear TNF. Either recombinant human TNF (n = 2; rhTNF) or bear plasma from 10 ng LPS treatment (n = 3; Bear + LPS) or bear plasma from RPMI treatment (n = 3; Control Bear) was combined with control antibody (black bar) or polyclonal antibody against mouse TNF (open bar). Control antibody had no effect on cytolytic activity of either human or bear TNF (low absorbance) whereas neutralizing antibody blocked TNF (high absorbance). Bars represent average absorbance ± SEM.

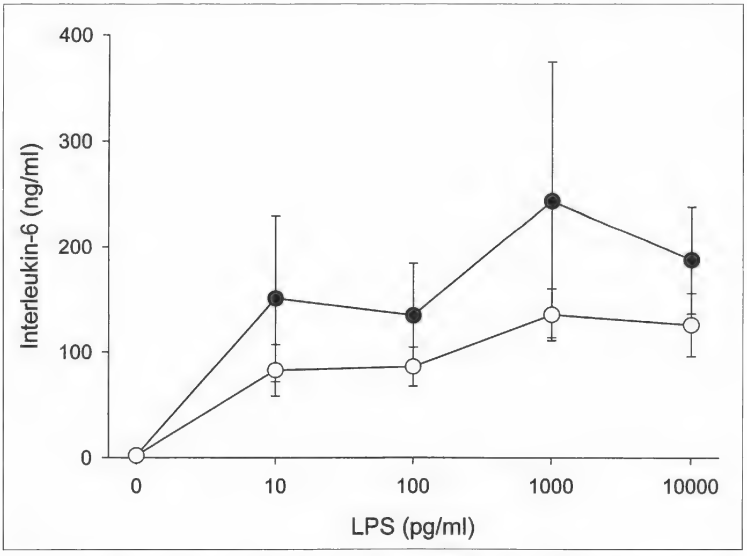

Figure 3. Absolute quantity of human IL-6 (black circle) and relative quantity of grizzly bear (open circle) IL-6 based on the B9 bioassay. Data (avg ± SEM) were collected from an LPS-stimulated whole blood experiments involving four replicate donors for both human and bear experiments. Quantity of IL-6 was based on serial dilutions of human recombinant IL-6 and may not reflect absolute concentrations of bear IL-6.

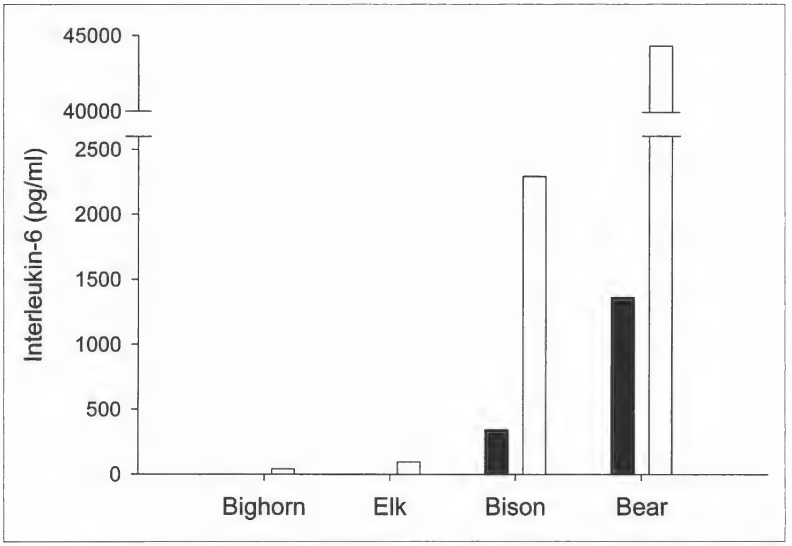

Figure 4. Demonstration of the feasibility of quantifying IL-6 for several wildlife species. Black bars represent control treatments (RPMI). LPS treatment (open bars) represent measurements from whole blood exposed to 10 mg LPS (bighorn sheep) or 50 mg LPS (all others) for six hours (n = 1 per species). IL-6 concentrations were estimated from serial dilutions of recombinant human IL-6.

IL-6 production. Some level of IL-6 was evident in all species of wildlife that we tested (Figure 4). As with the TNF assay, absolute quantification would require species specific standard curves. Despite this limitation, relative quantification in the context of experimental models could provide a rapid and simple means to quantify immunological responses to pathogens and toxins. *In vitro* blood experiments such as the ones described here could also be used to assess immunocompetence in free-ranging wildlife (Lochmiller et al. 1994).

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Isozyme Variation in *Sisyrinchium sarmentosum* (Iridaceae)

Abstract

Sisyrinchium sarmentosum is a rare, duodecaploid plant endemic to the Mt. Adams and Mt. Hood areas of Washington and Oregon. Isozyme variation in six Washington populations was assessed to infer genetic variation in this species. Five of the six sampled populations were monomorphic for the sixteen enzymes surveyed, although at one putative locus one of these populations was monomorphic for an enzyme band pattern not seen in any other population. The sixth population had low levels of variation in two enzymes. This low level of variation has often been observed in very rare species and high polyploids. Apparently, the species has recently gone through a bottleneck, perhaps during its recent origin as a species.

Introduction

Ideally, management practices designed to preserve rare plant biodiversity are based in part on an understanding of the population genetics of the rare species (Falk and Holsinger 1991). For practical reasons, such practices are usually based on the generalization that narrowly endemic species usually exhibit low genetic variation (Hamrick et al. 1991). However, individual endemic species vary widely in their genetic diversity (Karron 1991, Gitzendanner and Soltis 2000) and in the degree to which that variation is partitioned among populations (Hamrick et al. 1991). This study uses isozyme electrophoresis to characterize the genetic variation in the narrowly endemic, high polyploid plant, *Sisyrinchium sarmentosum* Suksdorf ex Greene, and to address some management-related questions.

Sisyrinchium sarmentosum, Pale Blue-eyed Grass, is endemic to a small area of south-central Washington and northern Oregon, in the vicinity of Mt. Adams and Mt. Hood (Henderson 1976, John Gamon pers. com.). Two thirds of the known populations occur in the Gifford Pinchot National Forest of Washington (Andrea Raven pers. com.). Its habitat includes mesic to wet meadows and forest openings at elevations of 480 to 1220 m (Gamon and Raven, pers. com). *Sisyrinchium sarmentosum* is characterized by glaucous foliage and pale blue, rather small flowers with tepals that are not emarginate (Henderson 1976). It reproduces vegetatively, spreading by rhizomes at least on a scale of many centimeters (Raven pers. com.). It also sets seed, and is highly self-compatible (Henderson 1976).

Sisyrinchium sarmentosum is a duodecaploid (12X) thought to have originated within the *S. idahoense* E. P. Bicknell complex (Henderson 1976). *Sisyrinchium idahoense* is widely distributed from British Columbia south to northern California, east to the Rocky Mountains. All Pacific Northwest *Sisyrinchium* species are tetraploid to duodecaploid (Henderson 1976). *Sisyrinchium idahoense* is usually octoploid (8X), but duodecaploid populations are known from central Oregon (Henderson 1976). No duodecaploid species or populations of *Sisyrinchium* are known to be sympatric with *S. sarmentosum,* but we are not aware of chromosome counts for *S. idahoense* from the range of *S. sarmentosum.* Artificial hybridization experiments indicate that many Pacific Northwest species are interfertile, and artificial crosses between *S. sarmentosum* and duodecaploid individuals of *S. idahoense* produce seed (Henderson 1976). Pollination among *Sisyrinchium* species results in seed set only when the pollen chromosome number equals or exceeds that of the ovule (Henderson 1976).

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Management-related issues led to this study. First, censusing of *Sisyrinchium sarmentosum* is complicated by the rhizomatous growth form of these plants. The inconspicuous shoots (ramets) can be counted, but many of them may belong to the same genetic individual (genet). Therefore, censusing genets is impossible, and the genetic effect of a reduction in the population of ramets is not obvious. Second, the observation that cattle eat and trample the flowering and fruiting stems of *S. sarmentosum,* significantly reducing seed set (Raven pers. com.), led to questions about the role of seed production in *S. sarmentosum* populations. Seed production affects both demographics and genetic diversity. Two demographic effects of seeds are obvious; they are the only method for producing new genetic individuals (genets), and seeds, rather than rhizomes, are the units of long-distance dispersal. The genetic effect of seed production in this vegetatively spreading, self-compatible, potentially long-lived, perennial plant depends on its genetic diversity, its breeding system, and the rate of seedling establishment. None of these factors is known for *S. sarmentosum,* but isozyme analysis can often shed light on the first two. An additional concern is the potential for outbreeding depression (Barnett and Kohn 1991) or blurring of species boundaries due to hybridization between *S. sarmentosum* and sympatric *S. idahoense.* Therefore, we evaluated the hypothesis that hybridization has occurred in the one *S. sarmentosum* population observed to be morphologically diverse.

Methods

This study used plants from the six populations of *S. sarmentosum* in the Gifford Pinchot National Forest that could be relocated and were large enough for sampling (Table 1). Leaves were collected in 1997 and transported on ice to the National Forest Genetic Electrophoresis Laboratory (NFGEL). Based on foliage color, the Little White Salmon River samples were believed to include *S. idahoense, S. sarmentosum,* and their hybrids. A tentative identification was recorded for each sample from that population.

Sample Preparation

Samples were prepared using standard NFGEL procedures (Anonymous 1995). A leaf sample approximately 8-11 cm long was ground in a cold mortar with 400 microliters of a Tris buffer pH 7.5 (Gottlieb 1981). The resulting slurry was transferred to wells in a microtiter plate and stored at –70 °C. In preparation for electrophoresis, slurry was thawed and absorbed onto 3 mm wide wicks prepared from Whatman 3MM chromatography paper.

TABLE 1. *Sisyrinchium sarmentosum* populations used in this study. All populations were located in Skamania County, Washington, in the Mt. Adams Ranger District of the Gifford Pinchot National Forest. "Outside" and "inside" refers to the location relative to the grazing exclosure at Cave Creek. Except as noted, the most important grazing animals were cattle. FS Rd. = Forest Service Road.

Population	Location	Latitude/ Longitude	Collection Date	Grazing Status	Sample Size
Cave Creek inside	north of FS RD 8631, ca. 0.5 mile south of the jct. of Rds. 8631 & 8620	45.9333°N 121.6437°W	2 July 1998	light for three years	35
Cave Creek outside	north of FS RD 8631, ca. 0.5 mile south of the jct. of Rds. 8631 & 8620	45.9333°N 121.6437°W	30 June 1998	Intense	35
Cayuse Meadows	ca. 400 feet north of Cayuse Meadow and west of Meadow Creek	46.1076°N 121.7892°W	24 July 1998	light (big game)	35
Little White Salmon River	small meadow south of FS Rd. 18, 0.25 mile south of jct. of Rds. 18 and 18.068	45.8317°N 121.6645°W	19 July 1998	light	35
Peterson Prairie	the northwest section of Peterson Prairie	45.9769°N 121.6645°W	9 July 1998	none until fall	35
South Prairie	north end of the prairie, ca. 0.6 mile south of junction of FS Rds. 860 & 8620.130	45.9188°N 121.7061°W	10 July 1998	light to moderate	35

Electrophoresis

Methods of electrophoresis followed the general methodology of Conkle et al. (1982) except that most enzyme stains are somewhat modified (Anonymous 1995). A lithium borate electrode buffer (pH 8.3) was used with a Tris citrate gel buffer (pH 8.3) (Conkle et al. 1982) to resolve the enzymes alcohol dehydrogenase (ADH), fluorescent esterase (FEST), leucine aminopeptidase (LAP), malic enzyme (ME), phosphoglucomutase (PGM), and phosphoglucose isomerase (PGI). A sodium borate electrode buffer (pH 8.0) was used with a Tris citrate gel buffer (pH 8.8) (Conkle et al. 1982) to resolve glutamate-oxaloacetate transaminase (GOT), glucose-6-phosphate dehydrogenase (G6PDH), triosephosphate isomerase (TPI), and uridine diphosphoglucose pyrophosphorylase (UGPP). A morpholine citrate electrode and gel buffer (pH 6.1) (Conkle et al. 1982) was used to resolve diaphorase (DIA), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), and phosphogluconate dehydrogenase (6PGD). All enzymes were resolved on 11% starch gels. Stain recipes for enzymes follow Anonymous (1995) except that GOT was stained using the recipe from Wendel and Weeden (1989). Two people independently scored each gel. When they disagreed, a third person resolved the conflict. For quality control, 10% of the individuals were run and scored twice.

Data Analysis

Sisyrinchium sarmentosum is duodecaploid (Henderson 1976). Therefore, in the most simple case, a single band may represent the activity of enzymes coded by six loci on 12 chromosomes. We treated each enzyme as if it were encoded by one putative locus, except that we treated PGI and TPI as encoded by two putative loci (actually two putative sets of homologous loci) each (Table 2). Therefore, we analyzed these data as if they consisted of sixteen isozymes (16 putative loci) (Table 2), referred to in the text and tables as sixteen enzymes. Gels were scored for banding pattern differences and band presence/absence. In this type of analysis, an enzyme banding pattern is considered a single phenotypic trait at which variation can be assessed.

Samples from the Little White Salmon River were analyzed as a single population of *S. sarmentosum*.

Phenotypic diversity measures were calculated from both band presence/absence and multi-band patterns (Table 3). For presence/absence data,

TABLE 2. Enzyme band pattern frequencies for *Sisyrinchium sarmentosum* populations. "Band Patterns" are schematic diagrams of bands observed for each pattern; 1 = presence of a band; 0 = absence of a band seen in other patterns of that enzyme.

Enzyme	Pattern	Cave Creek outside	Cave Creek inside	Cayuse Meadows	Peterson Prairie	Little White Salmon River	South Prairie	Band Pattern
ADH	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1111
DIA	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	11
FEST	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	11
GOT-1	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1
G6PDH	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1
IDH	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1
LAP	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1
MDH	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1
ME	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1
6PGD	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	11
PGI-1	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1
PGI-2	A	1.0000	1.0000	1.0000	1.0000	1.0000	0.9091	110
	B	0.0000	0.0000	0.0000	0.0000	0.0000	0.0909	111
PGM	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	11
TPI-1	A	1.0000	1.0000	0.0000	1.0000	1.0000	1.0000	01
	B	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000	11
TPI-2	A	1.0000	1.0000	1.0000	1.0000	1.0000	0.9118	1110
	B	0.0000	0.0000	0.0000	0.0000	0.0000	0.0882	1111
UGPP	A	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	11

TABLE 3. Genetic variation in *Sisyrinchium sarmentosum* populations, revealed by isozymes treated as sixteen putative loci. N = mean sample size/enzyme. %P = percent polymorphic putative loci; see methods for definition. P.I. = polymorphic index. S.W. = Shannon-Weaver diversity index. s.d. = standard deviation. "Outside" and "inside" refers to the location relative to the grazing exclosure at Cave Creek.

Population	N	# bands	# unique bands	% P	patterns/ locus	P.I	S.W.	% S.W. among populations
TOTAL	200	30	—	18.75	1.1875 (0.403)	0.3480	0.0387	0.1070
Cave Creek inside	35	27	0	0.00	1.0000	0.0000	0.0000	
Cave Creek outside	35	27	0	0.00	1.0000	0.0000	0.0000	
Cayuse Meadows	35	27	1	0.00	1.0000	0.0000	0.0000	
L. White Salmon River	26	27	0	0.00	1.0000	0.0000	0.0000	
Peterson Prairie	35	27	0	0.00	1.0000	0.0000	0.0000	
South Prairie	34	29	2	12.50	1.1250	0.3261	0.0377	
Mean/population	33	27	0.5	2.08	1.02	0.0544	0.0064	
s.d.	(3.6)	(0.82)	(0.84)	(5.1)	(0.051)	(0.133)	(0.015)	

phenotypic diversity was measured by a polymorphic index (PI), based on the frequency of occurrence of each band. For multi-band patterns, phenotypic diversity measures include: (1) the number of bands found in each plot, (2) percent of stains that yield more than one band pattern, (3) the average number of band patterns per stain in each plot, and (4) Shannon-Weaver Diversity Index values (Shannon and Weaver 1949). The Shannon-Weaver Diversity Index uses the frequency of each band pattern in each plot. The larger the Shannon-Weaver Index, the more diverse the plot. The distribution of the total variation within and among plots was determined by partitioning the total Shannon-Weaver Diversity Index. Band pattern frequencies and the Shannon-Weaver Diversity Index were calculated using Popgene (Yeh et al. 1997).

Isoelectric Focusing

Enzyme banding patterns in the Little White Salmon River populations were analyzed with isoelectric focusing (Acquaah 1992, Westermeier 1997). Methods of isoelectric focusing follow HyPure procedures (Anonymous 1994-1998). Tissue samples varied from 0.12 to 0.51 gram, prepared with proportional amounts of loading buffer. Polyacrylamide gels were stained for the enzymes acid phosphatase (ACP), diaphorase (DIA), esterase (EST), malate dehydrogenase (MDH), peroxidase (PER), and phosphohexose isomerase (PHI). Both buffers FS5480 (pH 3-10) and FS5080 (pH 4-5) were used to resolve ACP, EST, MDH, and PER. Buffer VG1110 (pH 3-7) was used for DIA and PHI. Buffer VG1080 (pH 3-10) was used for DIA, EST, MDH, PER, and PGM. Further information on buffer composition is available in Anonymous (1994-1998).

Results

Two adjustments were made to the data set before final analysis. One individual from South Prairie was removed from the analysis because it had unique patterns at 15 of the 16 enzymes sampled; it was presumed to be of a graminoid species rather than *S. sarmentosum*. Samples from the Little White Salmon River population were all treated as *S. sarmentosum* because their enzyme band patterns were all identical.

Although most isozyme patterns were simple and invariant, some enzymes exhibited multiple bands in all individuals (Table 2). Because of lack of variation in this species, band segregation could not be used to identify specific alleles and loci. Therefore, we treated the band pattern as the unit of analysis. However, each gel stained for PGI or TPI exhibited two regions of activity, which we considered to represent isozymes from different subcellular compartments (Gottlieb 1982). Therefore, we divided the PGI and TPI bands into two units. We refer to these units as putative loci.

Five of the six *S. sarmentosum* populations tested using starch-gel electrophoresis were monomorphic for all 16 enzymes examined (Table 2). One of these (Cayuse Meadow) was monomorphic

TABLE 4. Genetic variation in *Sisyrinchium* populations, revealed by isozymes, and in a rare *Iris*. N = mean sample size/enzyme. Pops = number of populations in the study. Enzymes = the number of different stains used. Loci* = the number of different regions on the gel treated as if they were loci. %P Enz. = percent of enzyme stains that revealed polymorphisms. %P = percent polymorphic putative loci or enzymes treated as loci; see methods for definition. Patterns/locus = patterns per putative locus. S.W. = Shannon-Weaver diversity index. Data for *S. montanum* and *S. septentrionale* reanalyzed as band patterns by the authors, with all high polyploid populations treated as *S. montanum*.

Taxon	N	Pops	Enzymes	Loci*	%P Enz.	%P	Patterns/ locus	S.W.	Source
S. montanum	36	5	13	24	61	54	1.9583	0.2661	Pavek 1989
S. sarmentosum	200	6	14	16	14	19	1.1875	0.0387	this study
S. septentrionale	6	1	13	24	46	21	1.2500	0.1417	Pavek 1989
Iris lacustris	229	9	10	22	0	0	1.000	0.0000	Simonich & Morgan 1994

for a TPI1 band pattern found in no other sampled population (Table 2). One population (South Prairie) was polymorphic at two enzymes, PGI2 and TPI2. Band patterns obtained were simple and consisted of a single band in 43% of the patterns. An additional 37% of the patterns consisted of two bands each, 10% were made up of three bands, and 10% were made up of four bands (Table 2). The Cayuse Meadows population had one unique band, and the South Prairie population had two. *Sisyrinchium sarmentosum* had very low levels of enzyme variation (Table 3). The levels of variation observed in this species was lower than that observed previously in *Sisyrinchium* species (Table 4).

In the Little White Salmon population, isoelectric focusing revealed approximately 186 bands, counting bands on each enzyme/buffer combination separately. Eleven (6.5%) of these bands were polymorphic (Table 5). No band differentiated the putative parental samples or the putative hybrids.

Discussion

A genetic interpretation of *S. sarmentosum* isozyme band pattern data would be preferred over a phenotypic analysis, because a genetic analysis provides information about population genetics and results can be compared directly with compilations of plant isozyme genetics (Hamrick and

TABLE 5. Polymorphic bands revealed by isoelectric focusing in the Little White Salmon population of *Sisyrinchium*. Sampled individuals are numbered. 1 = band presence; 0 = band absence. * = same band revealed on buffers VG1080 and FS5080. See Methods for enzyme abbreviations.

		S. idahoense											Putative hybrids												*S. sarm.*		
Enz.	Buffer	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	6	7	8	9	10	11	12	1	2	3
DIA	1080	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
EST	1080	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1
EST	1080	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0
EST	5080	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	1	1	0	1	1
EST	*	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1
MDH	5080	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
PER	5080	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1
PER	5480	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
PER	5480	1	1	0	1	1	1	0	1	1	1	1	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0
PHI	1080	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PHI	1110	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Godt 1990). Two factors made genetic interpretation of *S. sarmentosum* enzyme band patterns impossible. First, almost no bands segregated within or among populations, and therefore the number of loci and their relationships to specific alleles were difficult to judge. Second, uncommon alleles may escape detection because *S. sarmentosum* is duodecaploid (12X) (Henderson 1976). For example, the most obvious interpretation of a pattern consisting of a single band is that the genotype producing it is AA AA AA AA AA AA. However, the true genotype might be AA AA AA AA 00 00 if gene silencing occurs (Crawford 1990). In addition, the one visible band may result from the genotype AA AA AA AA AA AB if dosage regulation of gene expression occurs and limits the amount of enzyme produced from all these loci jointly. The enzymes produced by the B allele would be so rare compared to the enzymes produced by the A allele that they would probably not show up on the gel (AB heterodimers could be produced because of interlocus interactions, but these would still occur at a small frequency relative to AA homodimers, and therefore likely be invisible). If the plant is autopolyploid, an allele may be shared among all the homologous loci, and the plant might have a genotype such as AA AA AA AB BB (Soltis and Rieseberg 1986). If a two- or three-band pattern shows up occasionally, one must wonder how many copies of the alternative allele must be present, and/or how many null (silenced) alleles must be present, before the enzyme produced by that alternative allele can be observed. Phenotypic analysis provides a way of using isozyme data, such as that in *S. sarmentosum,* which cannot be interpreted genetically (e.g. Chung et al. 1991).

Enzyme variation in *S. sarmentosum* (as detected in starch gel electrophoresis) was extremely limited. Comparison with genetic analyses of plant isozyme data (Hamrick and Godt 1990) is instructive, if certain trends are kept in mind. First, the percent polymorphic enzymes is often higher than the percent polymorphic loci, because a single enzyme stain may reveal both variable and monomorphic loci. Second, the number of patterns reported per enzyme (or per putative locus) is often somewhat greater than the number of alleles per locus, because every combination of two alleles can produce a different pattern. Also, patterns are not independent. The addition of one allele for a dimeric enzyme will produce two additional bands. Third, the Shannon-Weaver diversity index may overestimate differences, because patterns produced by homozygotes are considered completely different from patterns produced by heterozygotes.

Sisyrinchium sarmentosum appears to have much less enzyme variation seen in the average narrowly endemic taxon (Hamrick and Godt 1990, Gitzendanner and Soltis 2000). For example, *S. sarmentosum* had 19% polymorphic enzymes, compared with the average of 26% polymorphic loci for endemic species, and 1.19 patterns per enzyme, compared to 1.80 alleles per locus in endemic species (Hamrick and Godt 1990). The variation in *S. sarmentosum* is also lower than that reported for other *Sisyrinchium* species of the Pacific Northwest, despite much smaller sample sizes in those other studies (Table 4), and the variation in those species was considered low (Pavek 1989). Like the monomorphic *Iris lacustris* Nutt. (Simonich and Morgan 1994), *Sisyrinchium sarmentosum* has characteristics (self-compatibility, restricted range, and moist habitat) associated with extremely low isozyme variation (Cole and Biesboer 1992).

Why are enzyme patterns in *S. sarmentosum* populations so nearly invariant? There are several possibilities. First, a high polyploid taxon that arose once would include a very limited sample of the genetic variation present in the parental species because it includes only the variation present in the one (or two) individual(s) that were parent(s) of the first high polyploid individual (Crawford 1990). Second, low population sizes for several generations would reduce variation, even if the population was initially variable. *Sisyrinchium sarmentosum* has had small populations and a very limited range since it was collected by Suksdorf (Gamon pers. com.). Third, low variation could characterize a species that reproduces entirely vegetatively. However, vegetatively reproducing taxa are often highly variable (Ellstrand and Roose 1987), and *S. sarmentosum* appears to reproduce sexually. It produces abundant seed when grazing does not prevent seed set (Raven pers. com.). The seed is probably produced sexually, because *S. sarmentosum* fails to produce seed in certain artificial crosses (Henderson 1976). A fourth hypothesis is that the observed low variation results from many generations of selfing. Selfing produces a preponderance of homozygous individuals,

but whether selfing populations are genetically variable or not depends on the variability of founding individuals and whether the population has gone through a prolonged period of low size. Some largely selfing populations are highly variable (Knapp and Rice 1996). We favor the hypothesis that duodecaploid *S. sarmentosum* arose once (or rarely) from an ancestor with lower chromosome number.

Sometimes isozyme analysis can determine if a species is an autopolyploid or allopolyploid, because allopolyploids usually exhibit fixed heterozygosity at many loci (Crawford 1990). *Sisyrinchium sarmentosum* has consistent multiple-band patterns for several enzymes, which may represent fixed heterozygosity at homologous loci. However, that does not help determine the origin of polyploidy in this species. The ancestor of *S. sarmentosum* was probably polyploid itself. We are not aware of information about the isozyme variation in *S. idahoense,* but duplicated loci were inferred for tetraploid *S. septentrionale* E. P. Bicknell (Pavek 1989). Duodecaploid *Sisyrinchium sarmentosum* may be an autopolyploid derived from an allopolyploid ancestor, but isozyme analysis of *Sisyrinchium sarmentosum* alone cannot eliminate other hypotheses.

The variation revealed by isozyme electrophoresis is not always representative of variation in physiology and other traits (Barrett and Kohn 1991, Hamrick et al. 1991), but there are several reasons to think *S. sarmentosum* has little genetic variation of any kind. The species shows less floral variation than most other Pacific Northwest species of *Sisyrinchium* (Henderson 1976). Morphological variation observed during recent field work is limited; single plants with white or twelve-tepaled flowers were observed in the Cave Creek population (Raven pers. com.), and foliage color varied only in the Little White Salmon River population. In addition, all populations occupy similar, open, wet to somewhat dry habitats within a very limited range. The apparent lack of genetic variation in *S. sarmentosum* does not imply that the species suffers inbreeding depression, because invariant plants may lack harmful genetic variants (Allard et al. 1986, Husband and Schemske 1997).

Variation in foliage color and tepal shape suggested that *S. idahoense, S. sarmentosum,* and their hybrids might have been collected at the Little White Salmon River site. That hypothesis was not supported by the results of this study. The plants all had the same enzyme bands as revealed by starch gel electrophoresis (Table 2). Isoelectric focusing of enzymes known to be highly variable and to exist in multiple forms revealed limited variation among individuals in this population but no consistent differences among the samples labeled as different species. If the sample identifications are correct, this uniformity of enzyme variation among species suggests that *S. sarmentosum* is the recently derived autopolyploid descendent of the widespread *S. idahoense.* However, the observed variation in foliage color may represent intraspecific variation in *S. sarmentosum.* Other *Sisyrinchium* species in the Pacific Northwest are known to exhibit variation in foliage color (Henderson 1976). This point could be clarified by additional research that included samples from single-species stands of *S. idahoense* and voucher specimens with flowers pressed in the field, to preserve the floral features necessary to confirm species identification (Henderson 1976).

Although the Shannon-Weaver diversity index indicates that populations of *Sisyrinchium sarmentosum* are little differentiated, gene flow among populations may be low (Table 3). All individuals in the Cayuse Meadow population had a band at TPI1 that was observed in no other population (Table 2). This situation could be stable only if gene flow between Cayuse Meadow and any other sampled population were very low.

Because *S. sarmentosum* had such low enzyme pattern variation and most populations were monomorphic, we cannot use enzymes to answer certain management-related questions. Enzyme patterns cannot delimit genets (clones), and therefore censusing genets remains problematic. Enzyme patterns cannot reveal the relative importance of sexual and vegetative reproduction in this species, and therefore decisions about protecting seed set cannot be made on the basis of enzyme patterns. The differentiation between the Cayuse Meadow population and the others hints at limited gene flow, suggesting that population establishment through long-distance seed dispersal events (which requires seed production) is important in the patterning of genetic diversity in this species. Perhaps different molecular techniques, such as isoelectric focusing, RAPDs, or ISSRs, can generate enough variation to address these questions more effectively.

The lack of observed variation suggests that few restrictions need be placed on programs to increase the *S. sarmentosum* population through transplants. Moving plants (seeds or rhizomes) among populations may be undesirable because it might lead to loss of rare genetic variations now restricted to single populations. However, as long as gene flow is as limited as it appears, establishment of new populations at sites not now occupied by *S. sarmentosum* need be restrained only by the pragmatic test that populations can be established only where the plants can grow.

This study suggests that preserving enzyme (and genetic) diversity in *S. sarmentosum* requires preserving many populations because some, like Cayuse Meadow, contain unique alleles. Also, a large population should be maintained at South Prairie, the only population known to be variable. However, this study also suggests that management practices directed toward demographics, rather than genetics, can be effective in long-term preservation of *S. sarmentosum* biodiversity. Unless populations are extremely small (<50), demographic changes are more important than loss of genetic variability for long-term population survival (Menges 1991, Schemske et al. 1994). This is especially true in a species such as *S. sarmentosum* that has little genetic variability.

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